EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

PUBLISHED BY

THE SOCIETY FOR THE STUDY OF EVOLUTION

Vol. VII **JUNE, 1953** **No. 2**

GENE FREQUENCY CHANGES IN SMALL LABORATORY POPULATIONS OF *DROSOPHILA MELANOGASTER* [1]

DAVID J. MERRELL

Department of Zoology, University of Minnesota, Minneapolis, Minnesota

Received September 4, 1952

INTRODUCTION

Recent concepts of the mechanism of evolution have stressed that evolutionary changes are fundamentally due to changes in the types and frequencies of genes in populations. The starting point for the study of the genetics of populations is the Hardy-Weinberg law, which shows that, in a random breeding population, in the absence of mutation and selection, the relative frequencies of the genes in the population will remain constant. The factors which have been recognized as instrumental in causing shifts in this equilibrium are mutation, in the broad sense of any hereditary change; selection, resulting in differential reproduction; population structure, which through isolation or migration, will affect the degree of inbreeding and crossbreeding; and population size, which, if small, may lead to rapid shifts due to genetic drift. The separate or combined effects of these quite different factors can all be expressed in terms of their effects on gene frequencies.

Some question still exists as to the importance and significance of genetic drift as a factor in evolution (Fisher and Ford 1947, 1950; Wright 1948, 1951). Since estimates of population size, gene frequency, and the many other variables in natural populations are difficult to make, experimental laboratory populations seemed a useful method for exploring the question. Several replications of one type of population can be studied under controlled conditions of temperature, light, and humidity, and the initial composition of the populations is accurately known. Furthermore, the problem is somewhat simplified by the elimination of migration pressure and of mutation pressure, which is small enough to be negligible.

METHODS

The problem of genetic drift was approached in the experiments to be reported through a study of small populations of *Drosophila melanogaster*. The technique used to raise suitably small populations was a modification of the population bottle technique described by Reed and Reed (1948). The flies were reared in two small homeopathic bottles with a combined volume of 32 cubic centimeters, which were held together by cotton bound with Scotch tape. Approximately 4 cubic centimeters of a standard corn meal, corn

[1] These studies were aided by a grant from the Graduate School of the University of Minnesota and by a contract with the Office of Naval Research.

syrup, agar, Moldex, and yeast mixture seeded with live yeast was added to each bottle. One of them was replaced alternately about every three or four weeks, at which time a count of the total adult population was made. The populations rarely exceeded 100 adults, and in many cases were down to less than ten flies. As might be expected, quite a few of the populations became extinct. Of a total of fifty-three populations started, twenty-seven died out. The losses were evidently at random because no differences were noted between the characteristics of the surviving populations and those which were lost.

Four sex-linked recessive genes, white (*w*), forked (*f*), yellow (*y*), and raspberry (*ras*) and the autosomal recessive glass (*gl*) were used. Each mutant was placed in competition with its wild type allele. For the sex-linked genes, the initial populations consisted of five mutant males, five of their wild type brothers, and five heterozygous sisters with a gene frequency of 0.5 for both alleles. These flies were obtained from crosses of heterozygous females to mutant males. Similarly with glass, five mutant males, five heterozygous males, and five heterozygous females formed each initial population, the mutant frequency being 0.67 in this case. No further effort to obtain uniformity of the rest of the genotype was made. Ludwin (1951) has shown that combinations of linked genes break up rapidly in populations due to crossing over, and each mutant pursues the same course in these populations that it does when alone in competition with its wild type allele. Therefore, it seemed unlikely that any combination of other genes might persist in these populations which would noticeably change the results from those obtained with flies which were more nearly isogenic. Furthermore, the selective disadvantage of the mutants was so great (except, perhaps, for forked) as to overshadow any minor differences existing at other loci.

TABLE 1. *Totals from 5 populations with yellow versus wild type*

Days	*N*	% wild phenotype	% males	q_m
0	75	67	66.7	.50
29	299	86	54.8	.26
60	72	79	55.6	.35
97	161	91	52.8	.16
122	39	92	51.3	.15
146	343	98	49.8	.04
173	41	98	41.5	.06
201	182	97	40.1	.07
232	31	97	48.4	.07
250	279	99	45.9	.01
270	272	99	51.1	.02

N = Total adult flies.

q_m = frequency of the recessive mutant in the males.

Both % wild phenotype and % males are percentages of *N*.

TABLE 2. *Totals from 7 populations with white versus wild type*

Days	*N*	% wild phenotype	% males	q_m
0	105	67	66.7	.50
25	630	71	55.7	.48
48	429	77	46.2	.41
67	113	90	37.2	.24
87	141	82	46.8	.21
112	189	88	51.3	.16
137	101	97	35.6	.11
161	353	96	47.3	.08
184	266	99	44.4	.02
212	133	100	44.4	—
241	63	94	47.6	.13
259	332	97	46.4	.06
279	441	98	56.2	.03

RESULTS

The effects of selection

The data can best be interpreted by treatment in several ways. Tables 1 through 5 summarize the data for each group of populations. The data for the individual populations are too extensive for publication, but are on file with the editor of EVOLUTION. Except in the forked populations, the frequency of phenotypically wild type flies rose quickly to above 90% and remained there. Thus, the overall results would indicate that

TABLE 3. *Totals from 4 populations with raspberry versus wild type*

Days	N	% wild phenotype	% males	q_m
0	60	67	66.7	.50
29	150	61	66.7	.48
58	100	82	55.0	.31
75	73	88	38.4	.32
94	127	92	46.4	.17
120	26	92	46.2	.17
143	248	96	46.8	.08
170	58	91	36.2	.19
198	175	94	41.7	.11
228	29	100	58.6	—
247	127	100	48.8	—
268	188	98	50.0	.03

selection favored the wild phenotype. Forked, in other experiments, has been found to have less of a selective disadvantage compared to its wild type allele than any mutant thus far studied, a result borne out in these experiments. As expected, most of the forked flies in the populations were males.

The trend toward elimination of the recessive gene can be followed further under the column q_m, which represents the proportion of males with a recessive sex-linked mutant. With sex-linked genes, the proportion of mutant males gives directly the gene frequency in the males, and this value can also be used as an estimate of gene frequency in both sexes. For yellow, white, and raspberry, a rather steady decrease in total frequency can be observed. No particular trend toward complete elimination of forked or glass can be observed in the estimates of their total frequency at each count. However, the frequency of both mutants remains consistently lower than the initial frequencies, which suggests that selection may also be functioning in these cases. The estimated gene frequency for glass was derived from the square root of the proportion of recessive flies of both sexes.

TABLE 4. *Totals from 5 populations with forked versus wild type*

Days	N	% wild phenotype	% males	q_m
0	75	67	66.7	.50
27	232	65	52.2	.54
56	64	75	39.1	.44
76	46	72	63.0	.41
99	224	80	50.0	.30
125	33	94	48.5	.12
150	168	74	51.2	.43
172	220	78	42.7	.43
201	58	74	44.8	.38
230	29	79	48.3	.43
249	316	78	52.8	.35
270	176	92	47.7	.11

TABLE 5. *Totals from 5 populations with glass versus wild type*

Days	N	% wild phenotype	q
0	75	67	.67
26	320	93	.26
48	289	95	.22
59	29	100	—
77	88	98	.15
100	194	100	—
125	49	98	.14
151	223	94	.24
173	256	97	.16
203	149	97	.18
231	84	92	.29
249	394	95	.22
270	251	94	.25
295	108	95	.22

N = total adult flies.
q = gene frequency of *gl*.

Forked, with quite good viability in the males, and not exposed to selection in the females because primarily carried by heterozygotes, was able to maintain a relatively high frequency. The flies homozygous for glass, however, were at a much greater selective disadvantage than forked flies. In large populations, with a large number of homozygous recessives, the rate of elimination of these homozygotes is quite spectacular. Its relatively high gene frequency was maintained because the gene was protected from selection in the heterozygotes of both sexes rather than only one. Phenotypically, the populations with *gl*

contained as many wild type flies as the populations of *y*, *w*, and *ras* where the gene frequencies were lower. There seems to be no need to postulate superiority of heterozygotes to account for the results with forked and glass. This question will be discussed further in a later paper. Thus, even in these small populations, selection can be observed to favor the wild phenotype.

The effects of small population size

The data for the individual populations reveal certain facts not discernible in the totals. Most striking, perhaps, are the large fluctuations in gene frequency which occur from one count to the next in so many cases. These results are in marked contrast to those obtained with larger populations in which the changes in frequency proceed in a more regular and gradual manner.

TABLE 6. *Comparison of observed and expected fluctuations in gene frequency between successive counts*

Yellow		White	
$(q_{n+1}-q_n)$	$\sqrt{\frac{q_n(1-q_n)}{2N_{n+1}}}$	$(q_{n+1}-q_n)$	$\sqrt{\frac{q_n(1-q_n)}{2N_{n+1}}}$
+.13	.107	−.18*	.042
−.24*	.041	−.04	.044
+.05	.064	+.60	.245
−.16*	.045	−.17	.060
+.09	.044	−.05	.028
−.04	.176	+.11	.049
−.36*	.054	+.21	.116
+.26*	.071	−.43*	.039
−.38*	.039	+.08	.047
−.02	.143	−.03	.052
−.24*	.060	+.14*	.037
		−.14	.154
		−.29*	.035
		−.03	.130
		+.08	.125
		−.06	.057
		+.03	.114
		+.60*	.155
		−.24	.087
		+.67*	.149
		−.10	.134
		−.21*	.041
		−.04	.049
		+.03	.051
		−.41*	.041
		+.05	.068
		+.05	.042

TABLE 6.—*Continued*

Raspberry		Forked	
$(q_{n+1}-q_n)$	$\sqrt{\frac{q_n(1-q_n)}{2N_{n+1}}}$	$(q_{n+1}-q_n)$	$\sqrt{\frac{q_n(1-q_n)}{2N_{n+1}}}$
−.06	.049	+.61*	.172
+.15	.091	+.01	.049
−.11	.138	+.57*	.157
+.21	.074	+.47*	.105
−.31*	.044	−.49*	.036
−.44*	.049	+.04	.249
−.20*	.041	+.87*	.107
−.11	.120	+.08	.063
+.25*	.076	−.11	.071
−.25	.158	−.10	.045
−.09	.047	+.54	.249
+.17	.069	+.02	.062
−.10	.046	+.21*	.017
−.33*	.102	−.23	.074
+.33	.133	−.10	.037
		+.57*	.010
		+.26	.180
		+.27*	.042

Glass	
$(q_{n+1}-q_n)$	$\sqrt{\frac{q_n(1-q_n)}{2N_{n+1}}}$
−.05	.041
+.16	.083
+.07	.079
−.03	.075
−.13*	.038
+.11	.066
−.01	.035
+.13	.075
−.04	.042
−.17*	.047
+.08	.061
.00	.032
.00	.025
+.17	.123
+.09	.040
−.06	.035
+.06	.046
−.07	.025

q = frequency of recessive gene.
n = count.
N = total adult flies.
* Statistically highly significant.

The observed fluctuations in gene frequency $(q_{n+1} - q_n)$ between count n and count $n+1$ have been drawn from the data on the 26 individual populations and are shown in Table 6. These values are compared with the standard deviations of

the expected fluctuations about q_n due to random sampling, which are equal to $\sqrt{\frac{q_n(1-q_n)}{2N_{n+1}}}$, N being the population size. These comparisons have been made only in those cases in which values of q are not equal to 0 or 1. The initial values were also excluded. It can be observed at once that the observed fluctuations are more than three times the expected standard deviation in about one third of the comparisons. Several factors are probably responsible for the unexpectedly large fluctuations. First, the effects of selection have not been eliminated. However, for any one generation these effects should not be great in comparison with the fluctuations. Second, the estimates of q for *y, w, ras,* and *f* are based only on the males. With *gl,* the estimates of q were based on both sexes, and only two observed values were significantly greater than expected. Third, the counts were usually made at about 20 to 30 day intervals. If the generation length were shorter than this, the fluctuations would tend to be increased. Fourth, if by chance, some flies produced fewer offspring than others or none at all, the effective population size would be smaller than the number counted, and the effect again would be to increase the size of the fluctuations. Hence, the effect of all of these factors is to increase the size of the fluctuations beyond the calculated values so that it is perhaps not surprising to find fluctuations of this magnitude.

Still another comparison will bring out the relationship between population size and fluctuations in gene frequency. The calculation of the expected variance in Table 6 was based on the population size of the progeny. The data, however, would seem to indicate that the size of the parental population also influenced the size of the fluctuations. Table 7 shows a comparison of the average size of the fluctuations in relation to population size of both the parents (N_n) and the offspring (N_{n+1}). The populations were arbitrarily classified in size as greater or less than 20, and again only fluctuations between values of q not equal to 0 or 1 were used. If the size of N_n had no influence on the size of the fluctuations there should be no significant difference between the fluctuations found when N_n is greater or less than 20. However, the average fluctuation was .107 $\pm$.022 when N_n and N_{n+1} were both greater than 20, but amounted to .206 $\pm$.033 when N_n was less than 20 and N_{n+1} greater than 20. The actual difference was 2.5 times the standard error of the difference and therefore statistically significant. This difference may be due solely to the fact that the estimate of q_n based only on the males is less accurate in such small populations, but it may also reflect some biologically significant effect.

TABLE 7. *Relationship between size of parent and progeny populations and size of fluctuation in gene frequency*

	Population sizes	Mean fluctuation in q
A	$N_n > 20$ $N_{n+1} > 20$	.107 $\pm$ .022*
B	$N_n < 20$ $N_{n+1} < 20$	.228 $\pm$ .041
C	$N_n > 20$ $N_{n+1} < 20$	.223 $\pm$ .045
D	$N_n < 20$ $N_{n+1} > 20$	.206 $\pm$ .033

As a result of these fluctuations, the various populations came to differ widely from each other in gene frequency. In no instance was this difference so great as that between a population homozygous for the mutant gene and a population homozygous for the wild type. Homozygosity of the recessive as a result of genetic drift seems to have been prevented by the action of selection. On the other hand, complete absence of mutant flies from some populations for long periods indicates the loss of the mutant from these populations at an early stage while in other populations the mutant remained present. These populations thus became qualitatively different from each other.

The data on individual *y*, *w*, and *ras* populations show that the gradual loss of the mutant apparent in the totals is due in part at least to complete disappearance of the mutant type from some of the populations but not from others. A succession of such losses at intervals gives the same appearance to the totals for each mutant as would a similar rate of loss in all populations.

Thus, in the small populations, random loss of the recessive genes has evidently occurred in several cases. Since the recessive gene was always lost and never fixed in the homozygous state, it is possible that the selection pressure against the recessive may have been intensified during the time when the populations were at their minimum size. Whether this be true or not, it seems probable that natural selection operated at all population sizes, small as well as large. When a population fluctuates in size (as these and most natural populations do), selection favors the wild type alleles while the population is relatively large. When it reaches a minimum, the wild type genes are already more frequent and selection still favors them. In addition, genetic drift now reinforces the action of selection since it generally tends to reduce still further the frequency of the less frequent allele in a population. Thus on the average, homozygosity for the more favored allele will be reached more rapidly in small populations than in large because of the combined effects of selection and genetic drift.

Discussion

These experiments show that initially similar small populations may diverge from one another in a short period of time. Genetic drift is sometimes thought of as a means by which a selectively disadvantageous allele may become fixed in a population. None of the recessives became homozygous in any of these populations. However, even though the mutants used are of good viability as laboratory stocks, they are genes of major effect and are clearly at a selective disadvantage compared to their wild type alleles. This is true even for the forked mutant, which in large populations over longer periods of time has decreased in frequency. The results with alleles more nearly equal in survival value or of small effect, such as the multiple factors which usually determine the differences between subspecies and species, may very well show that either allele can be fixed. However, the results indicate that even small populations do not exist in a vacuum entirely removed from the impact of natural selection. Unless some alleles can be identified which are neutral under all conditions, changes in gene frequency in small populations must be interpreted in terms of both selection and genetic drift. The relative importance of the two factors will vary according to the selection coefficient and the effective population size.

Summary

Gene frequency changes have been followed in small populations containing one of the sex-linked recessive genes *y*, *w*, *ras*, and *f*, or the autosomal recessive *gl* in competition with its wild type allele. Population sizes fluctuated approximately from 10 to 100 adults. Except for the forked group, the percentage of wild type flies rose rapidly and remained above 90%, indicating the phenotypic control of the populations by natural selection. Associated with this change was a gradual decrease in frequency of *y*, *w*, and *ras*. Both *f* and *gl* remained quite frequent, *f* because of its good viability, *gl* because carried in the heterozygous condition in both sexes. Large fluctuations in gene frequency occurred due to genetic drift, in some cases leading to loss of the recessive gene. The results are best interpreted as due to the combined effects of natural selection and genetic drift.

Acknowledgment

The author wishes to acknowledge the competent assistance of James C. Underhill in the maintenance and counting of the populations.

LITERATURE CITED

FISHER, R. A., AND E. B. FORD. 1947. The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* L. Heredity, **1**: 143–174.

FISHER, R. A., AND E. B. FORD. 1950. The "Sewall Wright Effect." Heredity, **4**: 117–119.

LUDWIN, I. 1951. Natural selection in *Drosophila melanogaster* under laboratory conditions. Evolution, **5**: 231–242.

REED, S. C., AND E. W. REED. 1948. Natural selection in laboratory populations of Drosophila. Evolution, **2**: 176–186.

WRIGHT, S. 1948. On the roles of directed and random changes in gene frequency in the genetics of populations. Evolution, **2**: 279–294.

WRIGHT, S. 1951. Fisher and Ford on "The Sewall Wright Effect." Am. Sci., **39**: 452–458.

CHROMOSOME PHYLOGENY AND HABITAT PREFERENCE OF *CLARKIA*

HARLAN LEWIS

University of California, Los Angeles

Received August 24, 1952

Phylogenies based upon morphological traits are often used to reconstruct the history or movements of taxonomic groups. But these phylogenies are limited by the fact that trends of only the most general sort can be established, because of the numerous factors involved. Phylogenies based upon chromosomal distinctions are more certain because the mechanisms which alter the structure and number of chromosomes are more simple and often result in linear relationships which can be determined with considerable rigor. For example, the chromosomal relationships between a number of species of *Drosophila* have been demonstrated (Patterson and Stone, 1952). Another outstanding example of a phylogeny based at least in part upon chromosomal consideration is that constructed by Babcock (1947) for the genus *Crepis*.

Clarkia,[1] a genus of annual plants, offers an unusual opportunity to examine phylogenetic changes in chromosome number at the diploid level in relation to ecological adaptation. The chromosome number of every known species has now been determined (Håkansson, 1941; Hiorth, 1941; Lewis, 1949; Lewis and Lewis, 1953; Lewis and Ernst, in press). Twenty-three species are diploid with basic chromosome numbers of 5, 7, 8, and 9. All of these are endemic to western temperate North America and the geographical distribution of each has been determined from extensive field observation and herbarium studies. It has been possible in the course of the field studies to compare the gross ecology of each species throughout most of their distribution areas. The breeding habit, population structure, and mechanisms of evolution in this genus have been discussed elsewhere (Lewis, 1953).

The original basic chromosome number of *Clarkia* is almost certainly 7, not only because its closest relatives have this number but also because cytological evidence indicates that genomes with 5 and 6 chromosomes have been derived from a higher number while those with 8 and 9 have resulted from the addition of the equivalent of whole chromosomes.

Clarkia is very similar morphologically to *Oenothera* and many species have been included in the latter by some taxonomists. *Clarkia* may have been derived from *Oenothera*. If not, the two genera have probably had a common ancestor. The basic number of all species of *Oenothera* that have been determined is 7 (Gates, 1928; Darlington and Janaki Ammal, 1945; Cleland, 1950; etc.) including representatives of at least 6 subgenera that I myself have determined. Furthermore, the species of *Clarkia* that most closely resemble *Oenothera* (*e.g.*, *C. amoena* and *C. rubicunda*) also have 7 chromosomes.

Genomes consisting of fewer than 7 chromosomes are known in two species. One of these, *C. amoena*, normally has 7 chromosomes but genomes with 6 are sometimes found in wild populations (Håkansson, 1942; Hiorth, 1942—as *Godetia whitneyi*). These genomes of 6 are apparently deficient and occur only as heterozygotes. However, Hiorth (1948a, 1948b) and Håkansson (1943, 1945, 1946) have shown beyond doubt that the genomes of 6 have been derived from the normal 7 through translocation followed by the loss of a centromere region, together, probably, with other small chromosome parts.

[1] *Clarkia* (Onagraceae) includes many species referred to *Godetia* by other authors.

The only other species with a haploid number less than 7 is *C. virgata* in which the basic number is 5. Its closest diploid relative, *C. mildrediae,* has genomes of 7 chromosomes. The chromosomes of these two species have not yet been studied in detail and their precise relationship is not known. However, the chromosomes of *C. virgata* are in general longer than those of *C. mildrediae.* This suggests that the genome of 5 chromosomes of the former has also been derived from 7 as a result of translocation and subsequent loss of centromeres as has been shown to have occurred in *Crepis* (Tobgy, 1943; Sherman, 1946).

Two-thirds of the diploid species have genomes of 8 or 9 chromosomes. These genomes have been shown in the cases studied to differ by the equivalent of whole chromosomes. The clearest example of a difference equivalent to a whole chromosome is that found between the normal haploid set of 8 chromosomes in *C. biloba* and a haploid set of 9 in the closely related species *C. lingulata* (Roberts, 1952; Lewis, 1953; Roberts and Lewis, unpub.).

An original number of 8 or 9 might be assumed for the genus. However, since the numbers greater than 7 apparently represent differences of whole chromosomes it would be necessary to assume a loss equivalent to one or two chromosomes in order to account for a genome of 7. All available evidence indicates that the effect of such gross losses in diploid individuals would certainly be lethal. Considering all evidence, the original chromosome number of *Clarkia* can reasonably be assumed to be 7 and the principal deviation has been an increase in chromosome number.

An increase in chromosome number at the diploid level may perhaps result from the acquisition of supernumerary chromosomes and their subsequent incorporation as an integral part of the genotype (Hiorth, 1947; White, 1945; Lewis, 1951). Supernumerary chromosomes which have the size and appearance of ordinary chromosomes and which in most cases behave like ordinary chromosomes are known in at least 5 species of *Clarkia* (Håkansson, 1945, 1949; Lewis, 1951). On the other hand, chromosomes which increase the basic number may perhaps be derived from interspecific hybrids. Meiotic irregularities in interspecific hybrids may produce viable gametes which include a complete genome of one parent plus an additional chromosome of the other.

The immediate morphological and physiological consequence of adding a chromosome to a genome will depend upon the genotype involved and may be relatively great or slight. However, regardless of the immediate effect, once an additional chromosome has become established the additional genic material thus acquired may not only increase the possibilities of recombination but may serve as a means whereby a great many mutations may become established which would not ordinarily be viable in a basic diploid. Such mutations, buffered by the genotype of the original basic complement, might eventually lead to the production of an organism very different from the original. Within the genus *Clarkia* constant differences in chromosome number are associated with species differentiation. However, it is conceivable that the addition of a chromosome might under appropriate circumstances not only set the stage for the evolution of a new species but also of a higher category.

An increase in chromosome number in *Clarkia* is correlated with habitat preference. The species with derived chromosome numbers are in general found in more xeric and probably more recent habitats. The ecological tolerance and area of distribution of each of the chromosome classes overlap conspicuously but the correlation between chromosome number and ecological adaptation is unmistakable.

The seven species with the original number of 7 chromosomes are found from central California to British Columbia, particularly in the mountains adjacent to San Francisco Bay, the northern Sierra Nevada, and the North Coast Ranges of California (fig. 1). The plant communi-

ties with which these species are associated can be taken as an index of their ecological preference. Five of them, *C. amoena, C. rubicunda, C. concinna, C. lassenensis,* and *C. mildrediae* are usually found in areas where the coniferous forest and woodland interdigitate. The first three are often found in openings in the redwood or Douglas fir forest but are more frequent in the oak-madroño woodland areas occupying the adjacent knolls and ridges. The last two species of *Clarkia* are more

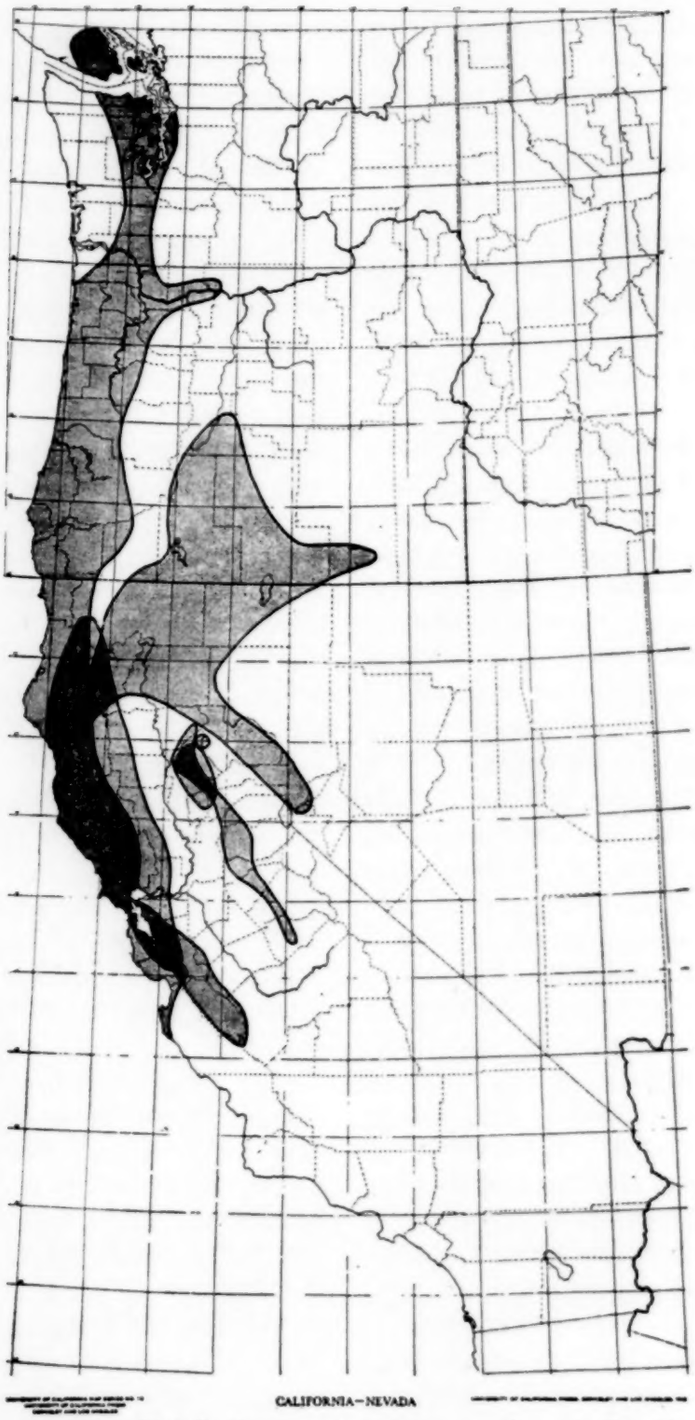


FIG. 1. Distribution of the seven species of *Clarkia* with a haploid chromosome number of 7, *C. amoena, C. rubicunda, C. lassenensis, C. arcuata, C. mildrediae, C. concinna,* and *C. breweri.*

interior and are associated with a forest of pine, Douglas fir, and black oak, but again in open sites and often in the adjacent woodland. Ecological sites similar to those occupied by these five species of *Clarkia* are of considerable antiquity. For example, the plant communities surrounding the Oligocene Florissant beds of central Colorado at the time of their deposition consisted on the one hand of *Sequoia* and other derivatives of the Arcto-Tertiary Flora. On the other hand, adjacent communities of evergreen oaks and other more arid derivatives of the Madro-Tertiary Flora were also present (MacGinitie, 1952). This suggests that species of

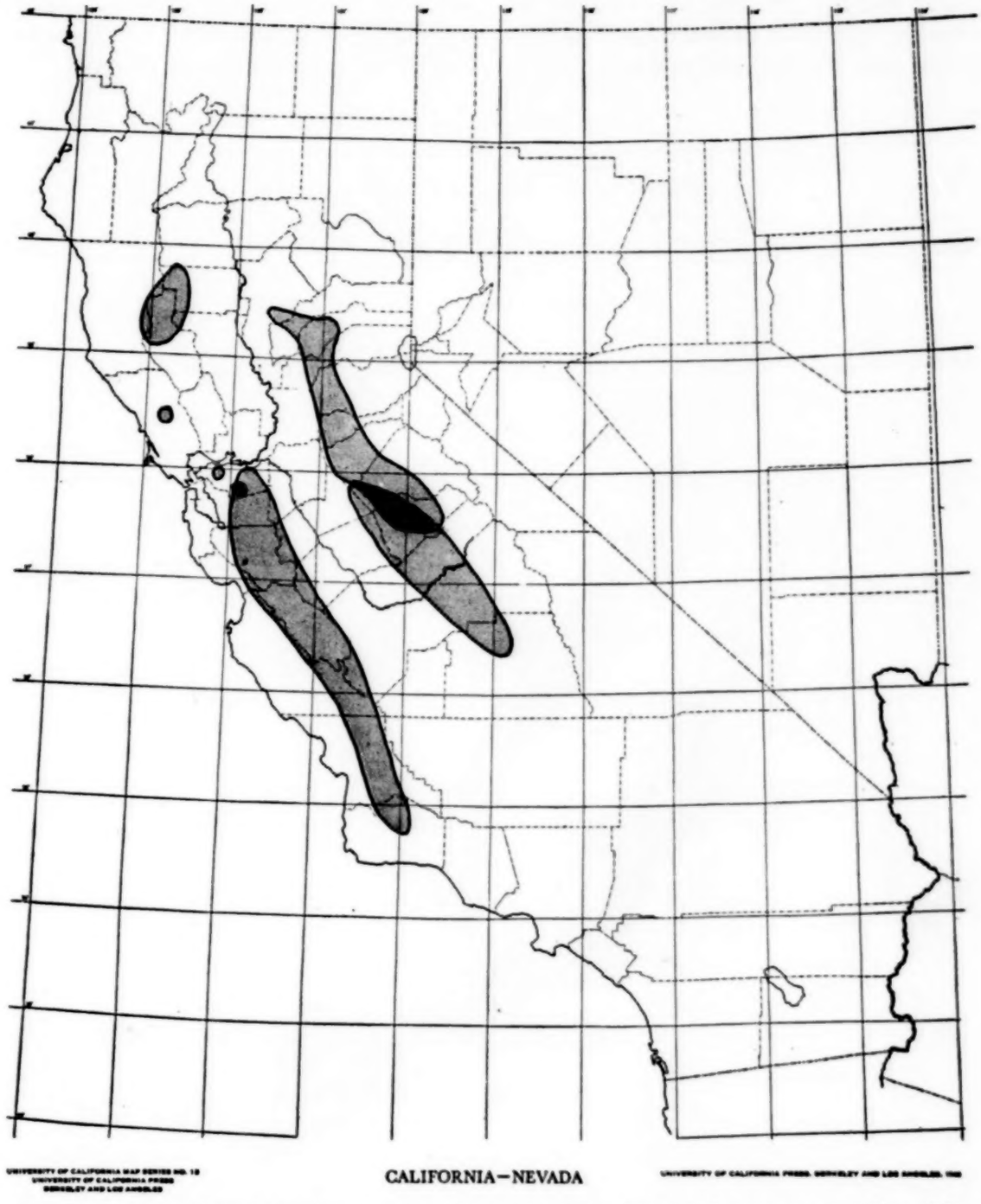


FIG. 2. Distribution of the three species of *Clarkia* with a haploid chromosome number of 8, *C. biloba*, *C. modesta*, and *C. imbricata*.

Clarkia with an ecological preference similar to those described above may also possess considerable antiquity.

Two species with 7 chromosomes, *C. arcuata* and *C. breweri,* are adapted to somewhat drier sites than the other species with the same chromosome number. These two species occur in the open oak-digger pine woodland in central California.

The three species with 8 chromosomes, *C. biloba, C. modesta,* and *C. imbricata,* all occur in oak-digger pine woodland in interior central California (fig. 2) in areas similar to those in which the most xeric

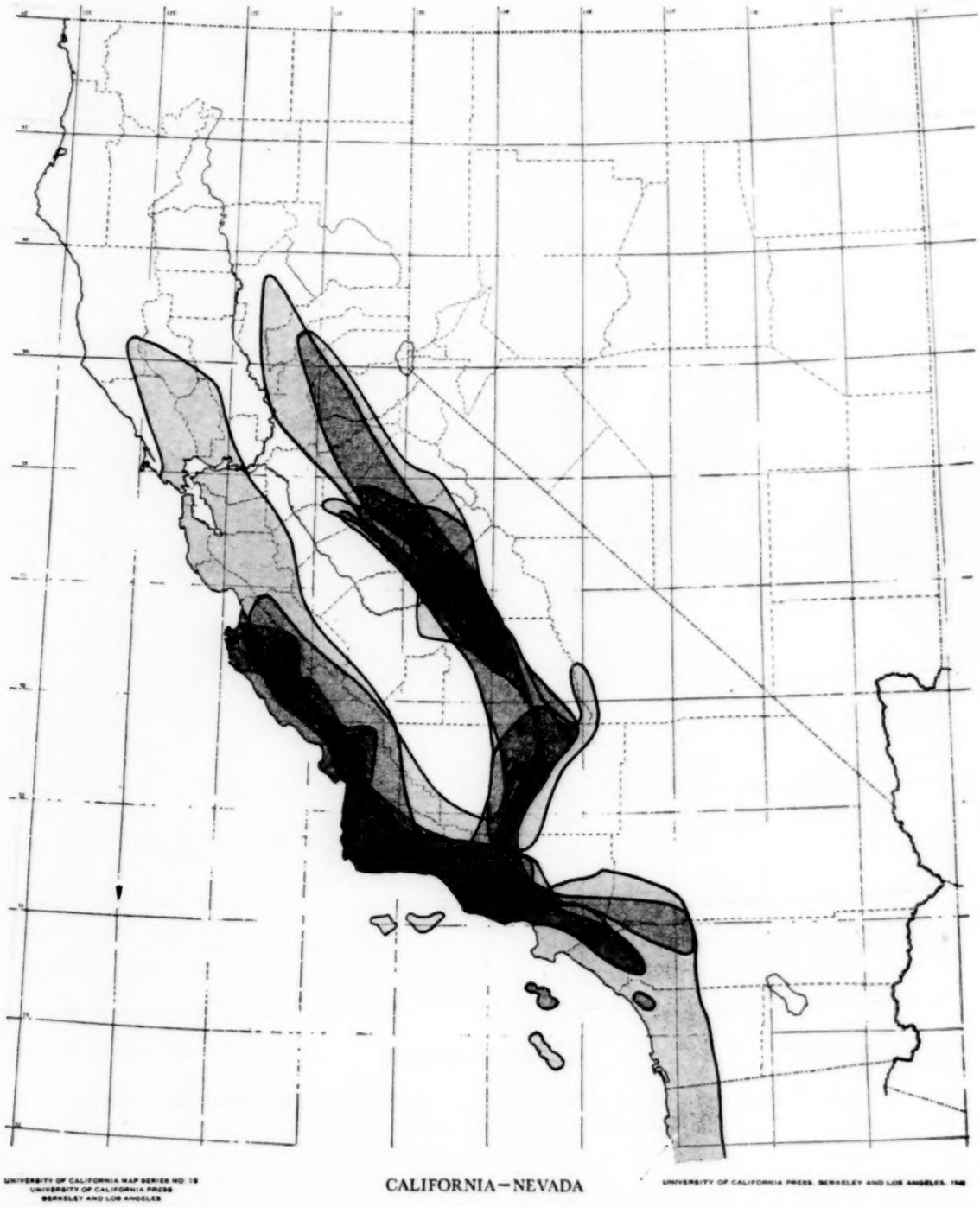


FIG. 3. Distribution of the twelve species of *Clarkia* with a haploid chromosome number of 9, *C. epilobioides, C. deflexa, C. bottae, C. cylindrica, C. unguiculata, C. xantiana, C. williamsonii, C. speciosa, C. dudleyana, C. lingulata,* and two undescribed species. *Clarkia epilobioides* also occurs in central Arizona.

species with 7 chromosomes are found. However, the distributions of the species with 8 chromosomes extend farther south and into drier areas than any of the species with 7 chromosomes.

The twelve species with 9 chromosomes are found primarily in the southern part of California, particularly along the margin of the arid San Joaquin Valley (fig. 3). All of these species occur to some extent in the woodland but most of them occupy the adjacent more xeric communities. *Clarkia unguiculata, C. dudleyana, C. williamsonii,* and *C. speciosa* are found predominantly in oak or oak-digger pine woodland although they frequently extend into adjacent communities. *Clarkia deflexa* and *C. bottae* are usually associated

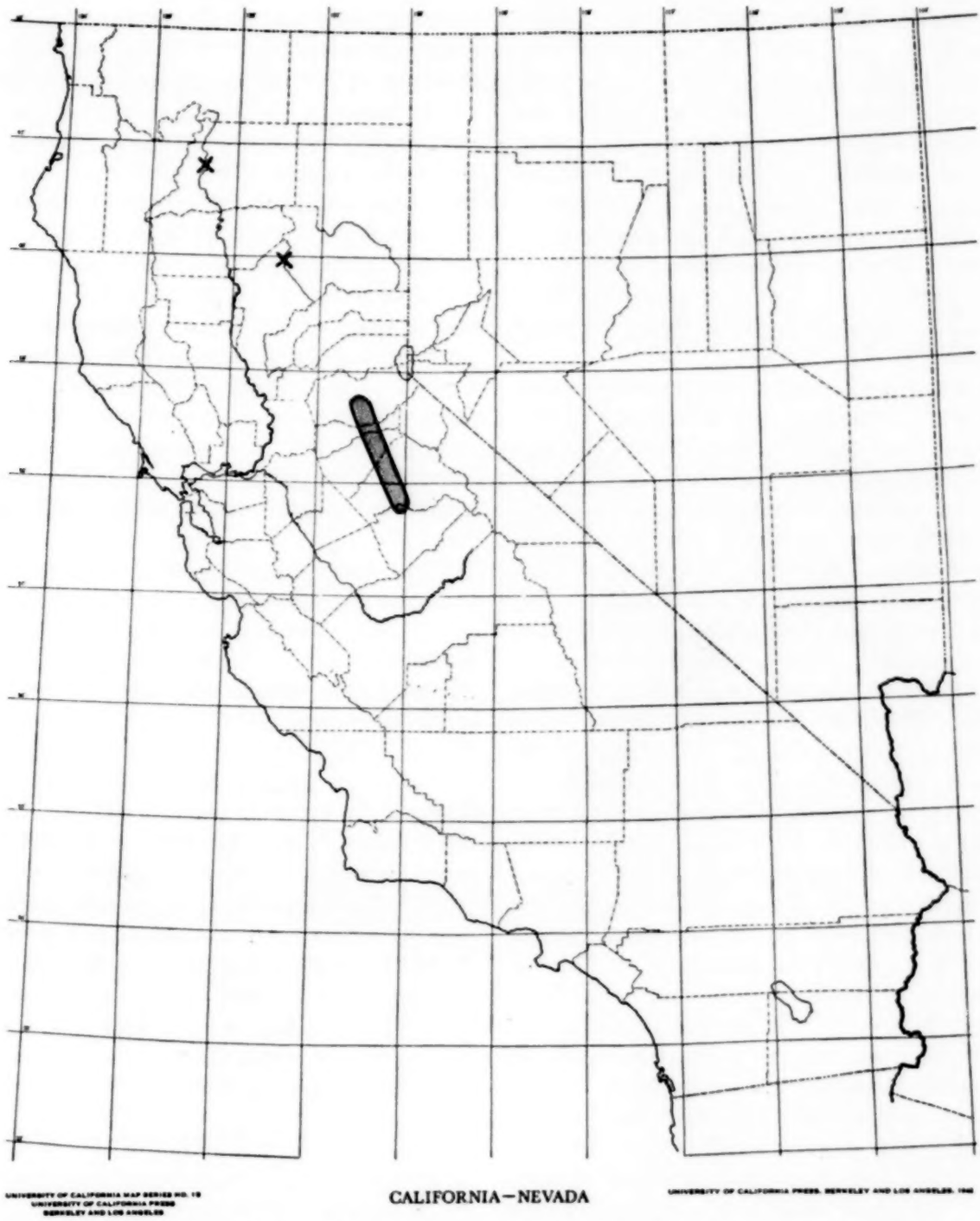


FIG. 4. Distribution of *C. virgata* (shaded area) with a haploid chromosome number of 5 and that of its nearest diploid relative *C. mildrediae* (X) with a haploid number of 7.

with the more xeric chaparral or coastal sage communities. *Clarkia lingulata* is known from only two colonies at the southern limit of distribution of its close relative, *C. biloba* with a basic number of 8. Both of the known colonies of *C. lingulata* are adjacent to chaparral. *Clarkia cylindrica* is most frequently associated with grassland as is also true of two undescribed species. *Clarkia xantiana* and *C. epilobioides* extend to the margin of the desert. The latter also occurs in central Arizona in an area dominated by Saguaro and Palo Verde. There is no question but that the species with 9 chromosomes are, as a group, adapted to considerably drier sites than the other diploid species of *Clarkia*.

The one species with 5 chromosomes, *C. virgata*, also occurs in a more xeric habitat and to the south of its nearest diploid relative, *C. mildrediae* which has 7 chromosome (fig. 4).

A change in basic chromosome number by way of increase, and in one case by decrease, has been associated with changes in ecological adaptation. The distribution of the various chromosome classes is apparently correlated with the water relations of the plant which in turn is associated with greater or less rainfall. But the precise way in which rainfall is limiting is unknown. The species concerned are annuals and might be expected to complete their life cycles during the season when rainfall is not limiting. We have as yet found no differences in the conditions required for germination of seeds, and suitable conditions are almost certainly met each year throughout most of the distribution area of the genus. Following germination the response to deficient rainfall within a given area appears to be the production of smaller plants with fewer flowers. However, considerable difference exists between species with respect to the length of time required to produce flowers under uniform garden conditions. In general, those species which occur in areas with the least and shortest period of rainfall are those which are first to flower (*e.g., C. epilobioides*) while those from more mesic habitats require a much longer period (*e.g., C. amoena*), but this correlation is far from absolute. Other factors are undoubtedly involved but these remain to be found.

The observed differences in ecological preference between chromosome classes may have accompanied the change in chromosome number or may have been subsequently acquired. Differences in ecological preference do exist, after all, between species in the same chromosome class, particularly in the oldest class with genomes of 7. However, the distribution of the various classes suggests a direct relationship between chromosome number and ecological tolerance. One can reasonably assume that the ancestral types were well-adapted to the areas in which they occurred. New genotypes which would accompany a change in chromosome number might stand small chance of being better adapted than the parents within the ancestral habitats. On the other hand, were these new genotypes adapted to somewhat different, in this case more xeric, conditions than the parents they might have an opportunity to become established and flourish.

The distribution of the chromosome classes and their ecological preference suggests that *Clarkia* originated from an ancestor with a haploid number of 7 chromosomes which was adapted to the more mesic aspects of an ecotone between the Arcto-Tertiary and Madro-Tertiary Floras, and that subsequent successful derivatives have been adapted to more xeric sites. This sequence seems particularly probable inasmuch as the greatest opportunity for establishment and expansion into new territories since the middle Tertiary in the area occupied by *Clarkia* has been into the more xeric communities derived from the Madro-Tertiary Flora which on the whole have been increasing in extent and diversity (Axelrod, 1948).

Summary

The original basic chromosome number of the genus *Clarkia* can be shown with reasonable certainty to have been 7. Subsequent change in chromosome number

has involved primarily the addition of the equivalent of whole chromosomes to produce genomes of 8 and 9. A reduction in number has also occurred as a result of translocation and loss of centromere regions.

Species with the original number of 7 chromosomes occupy for the most part relatively mesic sites while species with derived numbers occupy more xeric habitats. The correlation of chromosome phylogeny with ecological preference suggests that the genus may have had its origin in the more mesic aspects of an ecotone between the Arcto-Tertiary and Madro-Tertiary Floras and has subsequently spread into the more xeric derivatives of the Madro-Tertiary Flora.

Acknowledgments

I am greatly indebted to Professor Carl Epling for constructive criticism of the manuscript and to Professor D. I. Axelrod for several helpful suggestions. The Research Committee of the University of California has generously provided funds for the field work. Many of the cytological observations were made while the author held a National Research Council Fellowship in the Natural Sciences.

Literature Cited

Axelrod, D. I. 1948. Climate and evolution in western North America during middle Pliocene time. Evolution, **2**: 127–144.

Babcock, E. B. 1947. The genus *Crepis*. Univ. of Calif. Publ. Bot., Vols. 21 and 22.

Cleland, R. E. 1950. Studies in *Oenothera* cytogenetics and phylogeny. Indiana Univ. Publ. Science Ser. 16.

Darlington, C. D., and E. K. Janaki Ammal. 1945. Chromosome atlas of cultivated plants. Allen and Unwin, London.

Gates, R. R. 1928. The cytology of *Oenothera*. Bibliographia Genetica, **4**: 401–492.

Håkansson, A. 1941. Zur Zytologie von *Godetia*—Arten und-Bastarden. Hereditas, **27**: 319–336.

——. 1942. Zytologische Studien an Rassen und Rassenbastarden von *Godetia whitneyi* und verwandten Arten. Lunds Univ. Arsskrift N. F. Avd., **2**: 1–69.

——. 1943. Meiosis in a nullisomic and in an asyndetic *Godetia whitneyi*. Hereditas, **29**: 179–190.

——. 1945a. Zytologische Studien an monosomischen Typen von *Godetia whitneyi*. Hereditas, **31**: 129–162.

——. 1945b. Überzählige Chromosomen in einer Rasse von *Godetia nutans* Hiorth. Bot. Not., **1945**: 1–19.

——. 1946. Meiosis in hybrid nullisomics and certain other forms of *Godetia whitneyi*. Hereditas, **32**: 495–513.

——. 1949. Supernumerary chromosomes in *Godetia viminea*. Hereditas, **35**: 375–389.

Hiorth, G. 1941. Zur Genetik und Systematik der Gattung *Godetia*. Zeit. f. Vererb., **79**: 199–219.

——. 1942. Zur Genetik und Systematik der *amoena*—Gruppe der Gattung *Godetia*. Zeit. f. Vererb., **80**: 289–349.

——. 1947. Zur Genetik der Konfiguration 3-Kette + Univalent bei *Godetia whitneyi*. Biolg. Zentralblatt, **66**: 20–41.

——. 1948a. Über das Wesen der Monosomen und der disomen Anordnung 3-Kette + Univalent bei *Godetia whitneyi*. Zeit. f. Vererb., **82**: 1–11.

——. 1948b. Zur Genetik der Monosomen von *Godetia whitneyi*. Zeit. f. Vererb., **82**: 230–275.

Lewis, H. 1949. Chromosome numbers in *Clarkia* and *Godetia*. John Innes Hort. Inst. Annual Report, **1948**: 19.

——. 1951. The origin of supernumerary chromosomes in natural populations of *Clarkia elegans*. Evolution, **5**: 142–157.

——. 1953. The mechanism of evolution in the genus *Clarkia*. Evolution, **7**: 1–20.

Lewis, H., and M. Lewis. 1953. New species and changes in nomenclature in the genus *Clarkia* (Onagraceae). Madroño, **12**: 33–39.

Lewis, H., and W. R. Ernest. In press. A new species of *Clarkia* (Onagraceae). Madroño.

MacGinitie, H. D. 1952. Fossil plants of the Florissant beds, Colorado. Carnegie Institution of Washington Publ. 599.

Patterson, J. T., and W. S. Stone. 1952. Evolution in the genus *Drosophila*. Macmillan, New York.

Roberts, M. R. 1952. *Clarkia lingulata*, its origin and relationships, M.A. Thesis, Univ. of Calif., Los Angeles, Library.

Sherman, M. 1946. Karyotype evolution: a cytogenetic study of seven species and six interspecific hybrids of *Crepis*. Univ. of Calif. Publ. in Bot., **18**: 369–408.

Tobgy, H. A. 1943. A cytological study of *Crepis fuliginosa, C. neglecta*, and their F_1 hybrid, and its bearing on the mechanism of phylogenetic reduction in chromosome number. Jour. Genet., **45**: 67–111.

White, M. J. D. 1945. Animal cytology and evolution. University Press, Cambridge.

THE BALDWIN EFFECT

GEORGE GAYLORD SIMPSON
The American Museum of Natural History and Columbia University, New York

Received December 19, 1952

HISTORICAL INTRODUCTION

Characters individually acquired by members of a group of organisms may eventually, under the influence of selection, be reenforced or replaced by similar hereditary characters. That is the essence of the evolutionary phenomenon here called "the Baldwin effect."

The possibility of such an effect was noted independently and almost simultaneously by J. M. Baldwin [1] (1896), Lloyd Morgan (1896), and H. F. Osborn (1896). Lloyd Morgan (*e.g.*, 1900) and Osborn (*e.g.*, 1897a and b) made occasional later references to the effect (or factor, principle, or hypothesis, as you will). Baldwin (especially 1902) followed it up in greater detail. E. B. Poulton early joined the discussion, as did several others in the period 1896–1905, approximately.

That three workers independently thought of the Baldwin effect at the same time demonstrates that the idea was in the air, that it was an inevitable outgrowth of the intellectual atmosphere of the time. That time was at the height of the neo-Darwinian *versus* neo-Lamarckian controversy and shortly before the rediscovery of Mendelism gave a radically different turn to biological thought. There was a sharp issue, still familiar to all of us. Organism and environment obviously interact and obviously are closely fitted, that is, adapted to each other. Yet, as was already clear in the 1890's, it is improbable (to say the least) that the effects of the interaction can become heritable directly and in the same form. The Baldwin effect ostensibly provides a reconciliation between neo-Darwinism and neo-Lamarckism. To the extent that it may really occur, it provides a mechanism that is capable of making acquired characters hereditary—or of seeming to do so. Baldwin, Lloyd Morgan, and Osborn all explicitly postulated the Baldwin effect as a way out of the neo-Darwinian–neo-Lamarckian dilemma.

Mendelism and later genetic theory so conclusively ruled out the extreme neo-Lamarckian position that reconciliation came to seem unnecessary. After general acceptance of Mendelism and before clear statement of the modern synthesis of evolutionary theory, the Baldwin effect was seldom discussed in detail, although it continued to be mentioned under various names in reviews of evolutionary theory (*e.g.*, Delage and Goldsmith, 1912; Lull, 1917; Herbert, 1919). Huxley (1942) brought the "unduly neglected" Baldwin effect into the synthetic theory as a subsidiary factor. It is so recognized by most followers of the synthetic theory (*e.g.*, Mayr, 1951), although it is seldom assigned a major role in evolution.

In the meantime the notorious conflict about theories of genetics and of evolution was developing in the U.S.S.R. Until 1948 the most active and able Soviet biologists were contributing substantially to the synthesis of genetics and what was elsewhere usually called neo-Darwinism. There was, however, increasing ideological opposition to Mendelism and to theories of evolution that include random or indeter-

[1] James Mark Baldwin was born in Columbia, South Carolina, in 1861 and was educated at Princeton and under Wundt in Germany. He taught at several universities, including Princeton in 1893–1903 (the period of work on the Baldwin effect) and the Johns Hopkins, 1903–1908. After 1908 he spent some time in Mexico and finally settled in France, where he died in 1934. He was a pioneer in experimental psychology and an indefatigable writer and editor. His interest in evolution was part of a widespread effort to develop an evolutionary psychology. (See Boring, 1950; Langfeld, 1944.) Lloyd Morgan and Osborn are more familiar to evolutionists.

minate processes, as neo-Darwinism was accused of doing. The result was a conflict which because of its political apriorism must be called pseudo-scientific but which in form closely paralleled the genuinely scientific disagreement of the neo-Darwinians and neo-Lamarckians in the 1890's. In the U.S.S.R. the conflict was between Mendelism (associated with neo-Darwinism through the synthetic theory) and Michurinism (essentially the same as neo-Lamarckism). The similar situation had a similar result: Soviet students independently thought of the Baldwin effect. First was apparently Lukin around 1936,[2] and others followed up and strongly emphasized this trend of thought, notably Kirpichnikov (*e.g.*, 1947), Gause (*e.g.*, 1947), and Schmalhausen (*e.g.*, 1949).

As everyone knows, Michurinism was triumphant in the U.S.S.R., and Mendelism and neo-Darwinism were, in effect, outlawed in 1948. It is significant that particularly virulent attack was made on Schmalhausen's work, which embodied the Baldwin effect. The Baldwin effect could, as its earlier proponents had suggested, be considered as a compromise between the opposing schools, and compromise was ideologically even less acceptable than Mendelism.

Recourse has further been made to the Baldwin effect in still a third context: the conflicting philosophies of finalism (generally associated with vitalism) and materialism. As in neo-Darwinism *vs.* neo-Lamarckism and Mendelism *vs.* Michurinism, the evolutionary issue here centers on the problem of adaptation. Adaptation *seems* to be purposeful. The finalist view is that it is purposeful, in fact, but materialists generally rule out purpose as a possible factor in evolution. There are several possible materialistic explanations for seemingly purposeful adaptation. Among them is the Baldwin effect, which conceivably could, for instance, account for the genetic fixation of purposeful (or pseudo-purposeful) individual activities. The controversy between finalistic and materialistic philosophies of evolution has been especially active in France, and there Hovasse (1943) proposed what is essentially the Baldwin effect to account for adaptations considered finalistic by Cuénot (1941).[3] Hovasse (1950) later wrote a short book on the subject.

[2] *Fide* Gause and Schmalhausen. I have not read Lukin's publications, which are in Ukrainian and Russian.

Terminology and Definition

Baldwin called the effect in question "organic selection" and defined it as follows (Baldwin, 1902):

"*Organic Selection:* The process of individual accommodation considered as keeping organisms alive, and so, by also securing the accumulation of variations, determining evolution in subsequent generations."

In Baldwin's usage an "accommodation" was non-hereditary, *i.e.*, it was an acquired character, while a "variation" was (by definition) hereditary, *i.e.*, genetic. Thus his definition, somewhat ambiguous by present-day usages, designates a sequential process in which acquired characters are replaced by genetic characters. This is clear in Baldwin's discussion of the matter, which also brings in natural selection as the mechanism of replacement. Osborn and Lloyd Morgan accepted Baldwin's term with essentially his definition, and so have several later students, notably Gause. Others have used the term but not precisely with its original meaning. For example Lutz (1948) defines organic selection as "selection of the environment by the organism," a definition radically different from that of Baldwin and those who have followed him more closely.[4] The term is in any case misleading. "Organic selection" is no more organic than any other sort of selection. Moreover, the phenomenon discussed by Baldwin is not

[3] Cuénot's final (posthumously published) word on the subject (1951) was less decisively finalistic.

[4] Selection of the environment may, however, be a first step in the Baldwin effect, a possibility stressed by Thorpe (1945a).

directly or solely selection anyway. It is a complex process in which selection, strictly speaking, is only one of several factors, or it is an effect that is postulated as a result of selection.

Osborn used the term "coincident selection" alternatively as a synonym of "organic selection," the significance being that the "germinal variations" selected coincide with adaptive individual modifications. The same thought underlies Hovasse's preference for "parallel selection." Both terms are again misleading in that the process involves or results from but is not as a whole equivalent to selection, and "parallel selection" is liable to confusion with the wholly different process of parallel evolution (in two or more lineages) under the influence of natural selection. Schmalhausen and some others (mostly Russian) speak of "stabilizing selection." The term is sometimes equated with Baldwin's "organic selection," but the equation is misleading. "Stabilizing selection" applies literally and in Schmalhausen's usage to any mechanism tending to fix an adaptive type and to bring it under more rigid genetic control. The Baldwin effect is one such mechanism, but not the only one and not (even in Schmalhausen's opinion) the most important.

Those ambiguities and the difficulty of finding an apt descriptive term for so complex a process led Huxley (1942) to speak of the "Baldwin and Lloyd Morgan principle," [5] and Hovasse (1950) calls it "Baldwin's principle." That usage seems to me the simplest way toward a term both brief and unambiguous. Whether the mechanism or process in question is really a "principle" remains debatable, and I prefer the expression "Baldwin effect."

From Baldwin to Hovasse all those who have discussed the Baldwin effect under any name make it clear that what is meant is a complex sequence of events. The effect may be analyzed as involving three distinct (but partly simultaneous) steps:

(1) Individual organisms interact with the environment in such a way as systematically to produce in them behavioral, physiological, or structural modifications that are not hereditary as such but that are advantageous for survival, *i.e.*, are adaptive for the individuals having them.

(2) There occur in the population genetic factors producing hereditary characteristics similar to the individual modifications referred to in (1), or having the same sorts of adaptive advantages.

(3) The genetic factors of (2) are favored by natural selection and tend to spread in the population over the course of generations. The net result is that adaptation originally individual and non-hereditary becomes hereditary.

That description of the Baldwin effect is also a more precise definition of the term. At this point it need not be taken for granted that the effect actually occurs or has an essential role in evolution. It may be taken as a hypothesis subject to investigation.

Supposed Examples of the Baldwin Effect

The three processes involved in the Baldwin effect are all known to occur separately. The development of adaptive individual modifications or accommodations (sometimes called "somations") is widespread, a matter of common observation sufficiently established by the banal example of the strengthening of muscles by use. Partial or even complete correspondence between the effects of non-heritable modification and heritable mutations (broadly speaking) is also well-established in some instances. The phenocopies of Goldschmidt (1938) conclusively demonstrate this phenomenon. The existence of phenocopies, copying genetic effects without change in heredity, implies equally the existence of genocopies (Hovasse's apt term), copying non-genetic

[5] Even this length term fails to credit the simultaneous expressions of the principle, for Osborn thought of it as early as Lloyd Morgan and independently. When the coincidence was discovered, both Osborn and Lloyd Morgan deferred to Baldwin.

effects by change in heredity. That genetic effects, therefore also genocopies, can be spread through populations by natural selection requires no further substantiation at this late date.

Thus each process necessary for the Baldwin effect does factually occur. There is no reason to doubt that they could occur together, in the stated sequence, and so produce the Baldwin effect. There is even some probability that they must have produced that effect sometimes. Nevertheless two points remain decidedly questionable: whether the Baldwin effect does in fact explain particular instances of evolutionary change, and the extent to which this effect has been involved in evolution or can explain the general phenomenon of adaptation. Basis for judgment on these points is provided by brief review of some supposed examples.

Both Baldwin and Lloyd Morgan considered the Baldwin effect as a way in which, without transmission of acquired characters, habits and other learned behavior could become instincts, *i.e.*, inherited behavior. Their examples included the instinct (if such it be) of chicks to drink by throwing the head in the air, the instinct [6] in primates to grasp with the thumb opposed to the other fingers, and other examples of a similar sort. Osborn went so far as to suppose that an arboreal race of man could be developed by rearing infants in trees, where they would adaptively accommodate to the environment and where accommodation would eventually be replaced by "congenital variations." The soberer examples of Baldwin, Lloyd Morgan, and Osborn are usually open to the objection that when the characters in question are demonstrated to be hereditary there is no evidence whatever that they had occurred as accommodations before they became hereditary.

Somewhat more impressive is the example of bird song, already discussed at length by Lloyd Morgan (1896) and frequently mentioned by later authors. The characteristic song of some species of birds is learned by imitation. In other species the song is innate, hence presumably genetically determined, and in still others the situation is intermediate. It does seem possible, at least, that in some instances a learned song has become innate through the Baldwin effect. More direct evidence seems to be quite lacking, but that hypothesis has been accepted by Huxley (1942), among others.

Huxley also maintains that the Baldwin effect is usually involved in early stages of biological differentiation, that is, in the origin of races and eventually of species characterized by preferences for different hosts or food plants. Examples of such races are numerous as are also races distinguished in part by other behavioral and ecological preferences (see especially Thorpe, 1930, 1939, 1940, 1945a, b). Thorpe transferred insect larvae to new food plants, which the insects thereafter preferred, thus demonstrating that the preference may be caused by early conditioning. Other experiments, notably one by Harrison (1927), strongly suggested that natural selection of genetic variation was responsible for development of a strain with changed preferences: there was high initial mortality and only slow establishment of a population adapted to a new host plant. In that example individual modification perhaps also occurred, but the adaptation was mainly genetical. In sum the experiments by Thorpe and Harrison certainly show that adaptation to a new host may occur either by individual acquisition or by genetic selection, but they do not conclusively prove that hereditary adaptation *replaced* non-hereditary.

The most extensive experimental work on the subject is that of Gause (1947 and earlier work there cited). Asexually reproducing clones of the ciliate *Euplotes* showed individual accommodation by decrease of size when transferred from 2.5 to 5% salinity, and populations of excon-

[6] There are problems here as to whether these are instincts or reflexes, if there is a proper distinction between the two, and also as to whether the "instincts" of Baldwin and Lloyd Morgan were inherited as such and not at all learned.

jugants subjected to genetical selection under the same conditions showed a similar but more extreme response. Parallel results were obtained in adaptations of *Paramecium* to different temperatures. The results confirmed the possibility of the Baldwin effect, but I cannot agree that they demonstrated its occurrence. In fact the Baldwin effect did not occur in these experiments: they show, again, that similar adaptation may be produced either by non-hereditary modification or by genetical selection, but they do not show the latter replacing the former.

Gause's experiments brought out other interesting points. In a medium of 1% salinity *Euplotes* was viable but showed no individual modifications. In the same medium genetical selection among ex-conjugants resulted in increase in size. In 7% salinity pure, non-conjugating clones failed to accommodate and eventually died out, but selection produced strains genetically adapted to high salinity. In these experiments adaptation occurred, but only by genetical mechanisms. The Baldwin effect was definitely ruled out as even a possibility. The results bear on Hovasse's opinion that the Baldwin effect is a usual or necessary part of adaptation.

Hovasse (1950) goes so far as to say that "the application of this principle [the Baldwin effect] can lead to a general explanation of adaptation." The path to this extreme is acceptance at face value of all the criticisms of natural selection advanced on one hand by the neo-Lamarckians and on the other by the finalists. Each of those schools claims a general explanation of adaptation, and Hovasse accepts the generality but substitutes the Baldwin effect as mechanism. That is certainly going much too far. It seems to me to require no argument now that most of the neo-Lamarckian examples supposed to show inheritance of acquired characteristics are fully explained by ordinary natural selection without invoking the Baldwin effect or any other additional principle. Yet in a few cases, the prize exhibits of the neo-Lamarckians, the Baldwin effect does provide a plausible explanation not alternative to that of natural selection but showing how natural selection can have produced the observed result.

An example of this sort is the classic one of callosities still sometimes claimed as conclusive evidence for inheritance of acquired characters (*e.g.*, Wood Jones, 1943). Many vertebrates form calluses where the skin is habitually rubbed. The calluses are protective and may therefore be considered adaptive. They may be caused entirely by individual modification and are usually intensified, at least, by such accommodation. It has, however, long been observed that in some instances the calluses begin to appear in the embryo; for example, plantar calluses in man (Darwin, 1871), sternal calluses in the rhea (Cuénot, 1951), or elbow calluses in the wart hog (Leche, 1902). The Baldwin effect could explain this phenomenon. Such examples are perhaps most suggestive of a real role for the Baldwin effect in evolution, but they do seem too trivial to establish that role as universal or even particularly important.

Among the adaptive phenomena similarly considered crucial evidence by the finalists what Cuénot (1941) called "coaptations" are perhaps the most striking. In "coaptations d'accrochage" two parts of an organism arise separately in the embryo and subsequently fit together and have a single function. An example is the femoral groove of the mantis, into which the tibia is folded. (Numerous other examples are given by Cuénot, 1941; Corset, 1931; Hovasse, 1951.) To Cuénot coaptations were irrefutable proof of finalism. Hovasse agrees that they are inexplicable by mutation and natural selection and maintains that only "parallel selection," that is, the Baldwin effect, can explain them without recourse to finalism. The Baldwin effect may, indeed, be involved, but few will agree that it is the only possible non-finalistic explanation, and there is a glaring weakness in the argument. Again there is no good evidence that the coaptations (to the extent

that they are hereditary; they are not invariably or wholly so) did really begin as accommodations.

Hovasse goes still further. He attempts to meet all criticisms of natural selection by substitution of the Baldwin effect and so ends by making the Baldwin effect virtually all-powerful in adaptation. To give one more example, he cites the butterfly *Kallima,* which so closely mimics a leaf, and accepts the criticism that natural selection cannot have developed that mimicry because its advantage is all-or-none, not favored by selection until it is already established. Hovasse's own interpretation is that the ancestors of *Kallima* were changeable in color and pattern, that they actively copied leaves, and that this variable accommodation was finally fixed genetically by the Baldwin effect. This and some similar arguments seem to me so wildly improbable or, at best, so completely lacking in evidence that they merely weaken the whole case for the over-all importance of the Baldwin effect.

Status of the Baldwin Effect in Evolutionary Theory

The Baldwin effect is fully plausible under current theories of evolution. Yet a review of supposed examples and of pertinent experiments reveals no instance in which it indubitably occurred, no observations explicable only in this way, and few that seem better explained in this way than in some other. It probably has occurred, but there is singularly little concrete ground for the view that it is a frequent and important element in adaptation.

From 1896 up to now, everyone who has discussed it at any length has taken the position that the Baldwin effect is something distinct from natural selection acting on genetical variation and that its real importance is in meeting or explaining away the criticisms leveled at natural selection by, especially, the neo-Lamarckians, the Michurinists, and the finalists. The Baldwin effect is both possible and probable, but assignment to it of that role in evolutionary theory seems to me fallacious.

As an alternative to neo-Lamarckism or Michurinism, the Baldwin effect supposes that accommodation (adaptive somation) is paralleled by genetic changes with similar results. Actually this is no alternative at all and still leaves the basic decision to be made. If the Baldwin effect occurs, either there is or is not a causal connection between an individual accommodation and subsequent genetic change in a population. If there is no such connection, then the truly genetic change must occur wholly by mutation, reproduction, and natural selection, and the accommodation may be irrelevant. If there is a causal connection, the neo-Lamarckian argument is as much supported as supplanted. Indeed the claim (as by Hovasse) that the Baldwin effect is usual in adaptive evolution could be taken as an argument in favor of neo-Lamarckism: frequent coincidence of somation and mutation might suggest that one causes the other. Nor is the Baldwin effect an adequate answer to the arguments of the finalists, who can as readily see directive purpose in somation as in mutation.

The synthetic theory rests on grounds that have essentially nothing to do with the Baldwin effect. Occurrence of the Baldwin effect is nevertheless consistent with that theory and (if, indeed, it does occur) is an interesting but, I would judge, relatively minor outcome of the theory. It is simply one way in which natural selection may sometimes affect populations, and clearly it is not a factor either contradictory or additional to natural selection.

Of all those who have discussed the Baldwin effect, Schmalhausen seems to me to have most nearly placed it in true perspective within modern theories of evolution. Its place, not precisely in Schmalhausen's terms, may be summarized as follows. Genetical systems do not directly and rigidly determine the characteristics of organisms but set up reaction ranges within which those characteristics develop. An "acquired character" or specifically an adaptive modification (that is, an accommodation) necessarily occurs within a genetically determined reaction range. The

range may be relatively broad or extremely narrow. In any case an accommodation has genetical limits and develops only in the framework of the genetical system, but in a labile reaction range the particular form taken by a developing organism depends also on interaction with the environment. The genetical system evolves and the reaction range correspondingly changes. The range may come to cover different possibilities or it may become broader or narrower. If it becomes narrower, the possibilities for individual modification of characteristics become fewer. An accommodation that in a broader range occurs only as a specific response to a particular interaction with the environment may as the range narrows become the only developmental possibility. Then the Baldwin effect may occur: a response formerly dependent on a combination of genetical and environmental variables may become relatively or even absolutely invariable. It is not putting the matter in the right terms to say, as has usually been done, that this contrast is between "acquired" and "inherited" characters.

The ability to "acquire" a character has, in itself, a genetical basis. Selection acts (with some exceptions) on the phenotype, so that it is valid to say that selection is actually not on genetical characters but on the ability to acquire characters. This point is emphasized by an example recently discussed by Waddington (1952). The phenomenon involves, again, a broader principle of which the Baldwin effect may be considered a special case. The Baldwin effect would ensue when selection for the ability to acquire an adaptive character so narrowed the developmental range that the character would usually or invariably appear. There is, further, no evident reason why such selection might not act on genetical variation tending to push back appearance of the character into earlier developmental stages. Another aspect of the matter is that the genetical system producing such an effect may well differ in different instances. The absence, on both sides, of one-to-one correspondence of phenotype and genotype is well known. There is therefore wide possible scope for the Baldwin effect or especially for the phenomena of specialization and adaptation of which that effect is one aspect. All this does not seem to me to support the view of 'Espinasse (1952), who in discussion of Waddington's results concludes from the absence of such correspondence that the characters and adaptive changes of populations cannot usefully be interpreted in genetical terms. It only enriches and makes more widely explanatory such interpretation.

There is, finally, as Schmalhausen also pointed out, a certain balance between lability and stability of developmental ranges and norms in evolution. Wide ranges, with labile development, permit individual adjustment to the immediate environment and to short-term vicissitudes. Narrower ranges promote more highly specific and long-continued adaptation, usually advantageous under relatively constant conditions. Narrowing of the reaction range thus exchanges short-term and more plastic for long-term and more rigid adaptation. It is one of the aspects of specialization, and an important special case of evolutionary stabilization. Such a sequence need not precisely correspond with the Baldwin effect, but it includes that effect among the possibilities.

Seen in a modern context, the Baldwin effect helps to focus attention on a host of problems, especially in developmental (or physiological) genetics, well worthy of further study. It does not, however, seem to require any modification of the opinion that the *directive force* in adaptation, by the Baldwin effect or in any other particular way, is natural selection.

Literature Cited

Baldwin, J. M. 1896. A new factor in evolution. Amer. Nat., **30**: 441–451, 536–553.

——. 1902. Development and evolution. Macmillan, New York.

Boring, E. G. 1950. The influences of evolutionary theory upon American psychological thought. In, S. Person (ed.), Evolutionary thought in America: 268–298. Yale Univ. Press, New Haven.

CORSET, J. 1931. Les coaptations chez les insectes. Bull. Biol., suppl., **13**: 1–337.

CUÉNOT, L. 1941. Invention et finalité en Biologie. Flammarion, Paris.

——. 1951. L'évolution biologique. Masson, Paris.

DARWIN, C . 1871. The descent of man. Murray, London.

DELAGE, Y., AND M. GOLDSMITH. 1912. The theories of evolution. Huebsch, New York.

'ESPINASSE, P. G. 1952. Selection of the genetic basis for an acquired character. Nature, **170**: 71.

GAUSE, G. F. 1947. Problems of evolution. Trans. Connecticut Acad. Arts, Sci., **73**: 17–68.

GOLDSMITH, R. 1938. Physiological genetics. McGraw-Hill, New York.

HARRISON, J. W. H. 1927. Experiments on the egg-laying habits of the sawfly *Pontania salias* Chr. . . . Proc. Roy. Soc. London, (B), **101**: 115–126.

HERBERT, S. 1919. The first principles of evolution. 2nd ed. Black, London.

HOVASSE, R. 1943. De l'adaptation à l'évolution par la sélection. Hermann, Paris.

——. 1950. Adaptation et évolution. Hermann, Paris.

HUXLEY, J. S. 1942. Evolution. The modern synthesis. Allen and Unwin, London; Harper, New York.

KIRPICHNIKOV, V. S. 1947. The problem of non-hereditary adaptive modifications. Jour. Genetics, **48**: 164–175.

LANGFELD, H. S. 1944. James Mark Baldwin. Dict. Amer. Biog., **21**: 49–50.

LECHE, W. 1902. Ein Fall von Vererbung erworbener Eigenschaften. Biol. Zentralbl., **22**: 79–92.

LULL, R. S. 1917. Organic evolution. Macmillan, New York.

LUTZ, B. 1948. Ontogenetic evolution in frogs. Evolution, **2**: 29–39.

MAYR, E. 1951. Speciation in birds. Proc. Xth Int. Ornith. Congress: 91–131.

MORGAN, C. LLOYD. 1896. Habit and instinct. Arnold, London.

——. 1900. Animal behaviour. Arnold, London.

OSBORN, H. F. 1896. A mode of evolution requiring neither natural selection nor the inheritance of acquired characters. Trans. New York Acad. Sci., **15**: 141–142, 148.

——. 1897a. Organic selection. Science, Oct. 15, 1897: 583–587.

——. 1897b. The limits of organic selection. Amer. Nat., **31**: 944–951.

SCHMALHAUSEN, I. I. 1949. Factors of evolution. (Translated by I. Dordick; edited by Th. Dobzhansky.) Blakiston, Philadelphia.

THORPE, W. H. 1930. Biological races in insects and allied groups. Biol. Rev., **5**: 177–212.

——. 1939. Further studies on pre-imaginal olfactory conditioning in insects. Proc. Roy. Soc. London, (B), **127**: 424–433.

——. 1940. Ecology and the future of systematics. In, J. S. Huxley (ed.), The new systematics: 341–364, Oxford.

——. 1945a. The evolutionary significance of habitat selection. Jour. Animal Ecol., **14**: 67–70.

——. 1945b. Animal learning and evolution. Nature, **156**: 46.

WADDINGTON, C. H. 1952. Selection of the genetic basis for an acquired character. Nature, **169**: 278.

WOOD JONES, F. 1943. Habit and heritage. Kegan Paul, London.

GENETIC ASSIMILATION OF AN ACQUIRED CHARACTER

C. H. WADDINGTON

Institute of Animal Genetics, Edinburgh

Received October 9, 1952

INTRODUCTION

Under the influence of natural selection, development tends to become canalised so that more or less normal organs and tissues are produced even in the face of slight abnormalities of the genotype or of the external environment (Waddington, 1940). It has been suggested that if an animal is subjected to unusual circumstances to which it can react in an adaptive manner, the development of the adaptive character might itself become so far canalised that it continued to appear even when the conditions returned to the previous norm (Waddington, 1942). This mechanism would provide a means by which an "acquired character" in the conventional sense could be "assimilated" by the genotype, and eventually appear comparatively independent of any specific environmental influence. Schmalhausen (1947) has independently suggested a very similar process, which he has discussed at some length under the name "stabilising selection"; a phrase which, however, he uses in a number of different senses, as Simpson (1947) has pointed out.

The purpose of the present communication is to describe an experiment in which this hypothesis was tested and shown to operate as expected. A preliminary account of the work has been published in Waddington (1952a). The laborious work of classifying the large numbers of individuals involved was carried out by my technical assistant, Miss Evelyn Paton, to whose care and devotion I should like to pay a tribute.

EXPERIMENTAL RESULTS

1. Selection for response to an environmental stimulus

It was decided to select a strain of *Drosphila melanogaster* for its ability to form a phenocopy in response to some definite environmental stimulus. It was known from the work of many investigators that strains differ considerably in their capacities for phenocopy formation, and preliminary studies soon confirmed this. After some exploratory tests, it was found that when pupae of a wild Edinburgh strain, S/W5, were given a temperature shock (4 hours at 40° C.) at 17 to 23 hours after puparium formation, a fair number of crossveinless wings developed, although none appeared under normal conditions. It was decided to use this as the character to be selected. There is, of course, no reason to believe that the phenocopy would in nature have any adaptive value, but the point at issue is whether it would be eventually genetically assimilated if it were favored by selection, as it can be under experimental conditions. It was decided to concentrate on this effect, and to set up two separate selection lines. In one, only those flies which showed the crossveinless effect after treatment were bred from ("upward" selection, which should increase the frequency of response), while, in the other, the crossveinless flies were rejected, and only those still showing normal wings were used to carry on the line ("downward" selection).

In order to make it possible to collect enough contemporaneous pupae for treatment, a rather large number of individuals were dealt with in each generation. No attempt was made to ensure strict virginity in the females, but the bottles containing the selected strains were emptied every day and it is probable that a considerable proportion of the females were unmated.

Flies were classed as "crossveinless" when they showed any disturbance of the posterior crossvein. There was a considerable variation in the grade of expression of the character, ranging from the

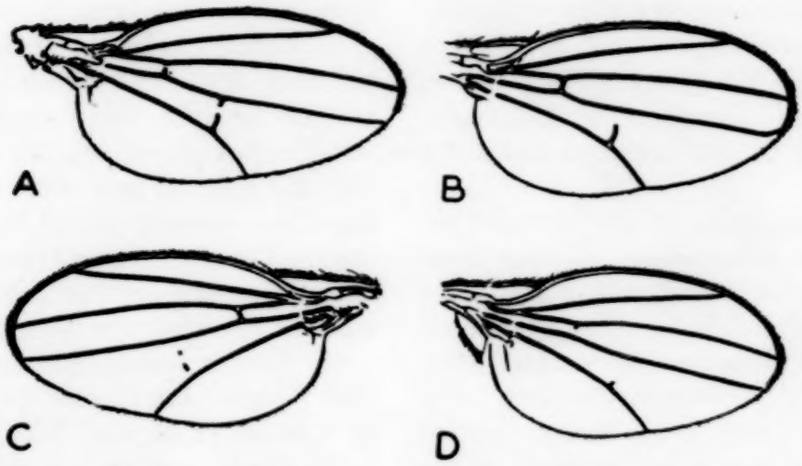


FIG. 1. Four crossveinless wings: *a* grade 4, *b* grade 3, *c* grade 2, *d* grade 1.

existence of only a small gap to a complete absence of the whole vein, sometimes accompanied by a breakage or absence of the anterior crossvein as well (fig. 1).

For the first few generations, the response to selection was somewhat irregular, although the downward selection, in particular, showed signs of being effective. A check with more restricted age groups then showed that the most effective period for the temperature shock was between 21 and 23 hours, and from the fifth selected generation onwards treatment was always given to pupae of this age. Selection in both directions then proceeded rapidly (table 1 and fig. 2).

Progress was, however, not steady in the downward line; from the sixteenth

TABLE 1

	Age treated	Upward line			Downward line		
		++	cve	%cve	++	cve	%cve
P1.	17–23	1466	747	33.8			
F1.	17–23	1582	470	22.9			
F2.	17–23	1727	502	22.5			
F3.	17–23	1784	521	22.6	1812	337	15.7
F4.	17–23	1312	738	36.0	1884	425	18.4
F5.	21–23	649	1070	62.2	1136	587	34.1
F6.	21–23	438	599	57.76	584	314	35.0
F7.	21–23	450	1009	68.5	1355	525	27.9
F8.	21–23	566	1618	74.1	1355	665	32.9
F9.	21–23	475	1308	73.4	1727	544	24.0
F10.	21–23	694	1674	70.7	2131	653	23.5
F11.	21–23	456	1808	79.9	1884	452	19.3
F12.	21–23	558	1583	73.9	1541	242	13.6
F13.	21–23	484	1510	75.7	1812	170	8.6
F14.	21–23	221	822	78.8	1082	90	7.7
F15.	21–23	165	630	79.2	1233	116	8.6
F16.	21–23	463	2598	84.9	2478	179	6.7
F17.	21–23	235	3521	93.7	2423	311	11.4
F18.	21–23	101	2567	96.2	2522	677	21.2
F19.	21–23	97	2387	96.1	2326	382	14.1
F20.	21–23	63	2564	97.6	2168	645	22.57
F21.	21–23	58	1804	96.85	1788	664	27.03
F22.	21–23	58	2277	97.52	1873	406	17.81
F23.	21–23	72	2133	96.73	2037	321	13.61

generation onwards, the frequency of phenocopies rose again, and attained a value about four times as high as it had at its lowest point. Thereafter it sank again. It is not easy to find an explanation for this.

In each generation of the upward selected line, a fair number of flies from untreated pupae were examined. No crossveinless individuals were found until generation 14, when a few isolated ones appeared. By generation 16 there were some 1–2% of these, and in that generation a number of pair matings were set up between them, the females being not certainly virgin. The condition was found to be inherited, and in the F1 from the original pairs, a number of new pair matings, with virgin females, was made, in some cases between crossveinless pairs and in others between normals. Thus from each of a number of original non-virgin pair matings, a series of lines were started.

No useful purpose would be served by giving the detailed figures for the inheritance of the crossveinless condition in all these lines. The frequency of the character, under conditions of normal culture at 25° C. (with of course no temperature shock) varied from about 75% to a very low frequency. In different sub-lines, derived from the same original non-virgin pair, matings between normals gave significantly fewer crossveinless flies than did matings between crossveinless. Over the whole series of matings, the difference was 18.5 ±4.5%. There was thus still considerable genetic variability within the lines. The interaction term was also significant, so that the variability within lines was not the same for all lines.

By further selection among these lines, four "high" lines were produced (Nos. H 1, H 16, H 24, and H 26), which threw fairly high percentages of crossveinless flies at 25° C. with no temperature shock. A similar number of "low" lines were also isolated, either from among the strains mentioned above or by new matings among the normals appearing among the treated upward selected strain. These low lines (Nos. L 4, L 8, L 25, and L 28) gave very low percentages of crossveinless individuals, although they were derived from the upward selected group and must have shared most of their genetic background with it.

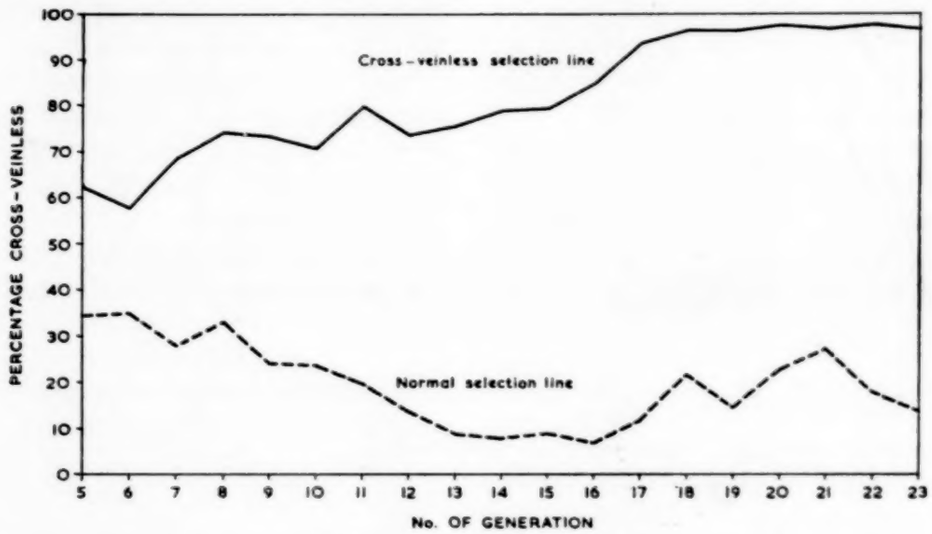


FIG. 2. The response to selection, from generation 5 onwards, for crossveinless wings ("upward" selection) and normal wings ("downward" selection).

The frequency of spontaneous crossveinless flies (*i.e.*, developed in the absence of a temperature shock) is given for the various lines in figure 3. The rather odd fact will be noticed that the frequency is higher at 18° C. than at 25° C., which might

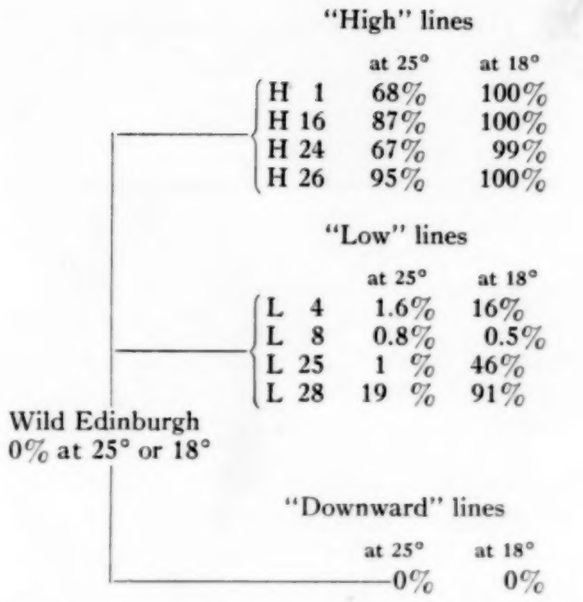


FIG. 3. Frequencies of crossveinless phenotypes in the various lines.

hardly be expected as the phenotype originated as a phenocopy induced by a high temperature shock treatment; but there is no reason why the effects of temperature shock treatment should be paralleled by those of temperature variations within the normal range. The frequencies quoted in the figure were determined shortly after the lines had been set up. The strains were carried on by non-virgin matings of crossveinless for the high lines and non-virgin matings of normals for the low lines. After seven or eight generations, the frequencies of crossveinless individuals at 25° C. were determined again, and

TABLE 2. *Grades of expression (in percentages)*

	1	2	3	4	Normal	% cvl
High lines (carried by non-virgin matings of cvl).						
H 1	9	46	18	20	6	94
H 16	20	46	19	13	2	99
H 24	0.5	17	23	37	23	77
H 26	2	38	22	33	5	95
Low lines (carried by non-virgin matings of normals)						
L 4	—	—	—	—	100	100
L 8	—	—	0.4	0.8	99	1.2
L 25	—	—	1	0.5	98.5	1.5
L 28	3	14	14	25	44	56

are given in table 2, which also gives the grades of expression in terms of an arbitrary classification (see fig. 1). It will be seen that most of the lines have remained fairly stable, or have progressed in the direction of the rather feeble selection applied, except in the case of low line L 28, in which the frequency of crossveinless has considerably increased. It may be noted that this was a strain extremely sensitive to temperature at the earlier stage in its existence (fig. 3); but the explanation for its behavior in the intervening seven generations remains obscure.

2. *Genetic analysis of the lines*

Crosses with wild types: A series of matings were made between females of various high lines and males of different

TABLE 3. *F1's and backcrosses of high lines with various wild types*

Original cross. ♀	♂	F 1 cvl	F 1 Total	F 1 %cvl.		Backcross ♀♀ × ♂♂ cvl	Backcross ♀♀ × ♂♂ Total	Backcross ♀♀ × ♂♂ %cvl.
H 1 (68%)	D (0%)			?		854	1426	60
H 16 (87%)	D (0%)			?		1645	2942	56
H 24 (67%)	D (0%)			?		313	628	50
H 26 (95%)	WE (0%)	14	234	6	(ex cvl ♀)	96	153	63
					(ex + ♀)	847	1342	63
H 1 (68%)	L 4 (4%)	29	37	80		425	610	70
H 16 (87%)	L 25 (8%)	10	44	24		117	153	76
H 24 (67%)	L 28 (6%)	28	45	62		219	255	86
H 26 (95%)	L 8 (4%)	27	107	26	(ex cvl ♀)	94	148	64
					(ex + ♀)	171	238	72

wild types. The F1 females were then crossed back to males of the original high line. The flies were reared at 18° C. The results are given in table 3, in which the percentage of crossveinless given at 25° C. by the lines used for the cross are indicated in brackets. Unfortunately the F1's of the cross between high lines and downwardly selected stocks (indicated as D, first three rows) were not noted, but the frequency of crossveinless was certainly very low.

It will be seen that the general genetic background of the wild types has a considerable effect on the frequency of crossveinless. In the background of the low lines, which are more or less true breeding wild types derived from the upwardly selected strain, the condition behaves almost as a dominant, while against the downwardly selected background it is nearly a complete recessive. Against the Wild Edinburgh stock from which the experiment started (W.E.), it shows a slight degree of dominance. This is not surprising if the genes concerned in producing the crossveinless phenotype behave in an additive manner, but, in the original Wild Edinburgh stock, are never present in sufficient concentration to overtop some crucial threshold.

Crosses with chromosome markers: The experiments described in the last paragraph show that many genes—in fact the genetic background as a whole—affect the penetrance of the character. In an attempt to locate at least crudely the more important factors, high line females were crossed with the Curly Moire males, and Curly Moire F1's bred together in pairs. There were about 10% crossveinless flies in the F1, which was reared at 25° C. The numbers of crossveinless appearing in the various classes of the F2 (also reared at 25° C.) are given in table 4. It will be seen that the original percentage of crossveinless is never recovered in the non-Cy non-Me offspring, from which it would appear that the X chromosome of the high lines is the bearer of important genes tending to cause the condition. Penetrance is highest in the Cy group,

TABLE 4. *Percentages of crossveinless*

H ♀ × Cy Me ♂

|

F1 Cy Me's crossed (at 25°)

		$\frac{Cy}{HII}, \frac{Me}{HIII}$	$\frac{Cy}{HII}, \frac{HIII}{HIII}$	$\frac{HII}{HII}, \frac{Me}{HIII}$	$\frac{HII}{HII}, \frac{HIII}{HIII}$
H 1	68	16	60	19	49
H 16	87	24	89	17	72
H 26	95	15	66	15	60

and lowest in the Me. This suggests that the high line IIIrd chromosome has more crossveinless effect that the Me, while the high line IInd has less than the Cy. This would also account for the fact that more affected flies are found among the Cy's than in the non-Cy non-Me group.

A further test of the effect of the IIIrd chromosome was made by crossing H 26 females to Wild Edinburgh males; then mating an F1 male to Stubble females. The resulting Sb males are without a high line X, and are heterozygous either for a high line IIIrd or a Wild Edinburgh IIIrd, It was hoped that when individual males were crossed to high line females, the families would fall into two groups with respect to the frequency of crossveinless among the non-Sb offspring, and thus demonstrate a clear cut difference between the high line and Wild Edinburgh IIIrd chromosomes. In fact, the frequency of crossveinless (at 18° C.) was 59% among the non-Sb and 37.5% among the Sb. It is true that the families were non-homogeneous as regards the frequencies among the non-Sb, but unfortunately so were they as regards those among the Sb. Probably this can be attributed to effects of the high line IInd chromosomes. It may be noted, however, that non-Sb group had a higher overall frequency than the Sb, confirming the suggestion that the high line IIIrd, which about half the non-Sb's would contain, has a positive effect in producing the crossveinless type.

The effect of the high line X was tested in a similar manner. Females heterozy-

gous for an H 26 X and the Muller-5 chromosome were crossed with low line males. In the Muller-5 male offspring reared at 25° C., only 2 crossveinless flies were found among 480, while among the non-Muller-5 males the frequency was about 40%. There is therefore a very definite crossveinless effect of the high line X.

Similarly when females heterozygous for high line X and Muller-5 are crossed with high line males, the Muller-5 male offspring showed no crossveinless among 348 at 25° C. and 18 among 513 (3.5%) at 18° C., while the non-Muller-5 males had 193 among 447 (43%) at the higher temperature and were 100% crossveinless at the lower.

There is of course a well known crossveinless factor at locus 13.7 in the X, and it is interesting to discover whether the effect of the high line X is due simply to an allele of this. In the stocks available in Edinburgh, the known cv factor shows no obvious signs of temperature sensitivity, giving 100% crossveinless flies at 25° C. as well as at 18° C. Heterozygous *sc cv ec ct/high line 26,* however, were by no means 100% crossveinless at 25° C., the number of wild types being 48 in 228 when *sc cv ec ct* was the female parent and 55 in 166 when it was the male. There is clearly considerable summation of the effects of single doses of *cv* and of the high line X, but the latter does not act as if it contained a simple allele of the former.

Moreover, it can be shown that there is a tendency to produce crossveinless flies in regions of the high line X far removed from the locus of *cv*. Heterozygous *sc ct v f car/high line 26* females by *sc ct v f car* males gave, of course, a large number of types of cross-over. The frequency of crossveinless among the non-cross-overs and single cross-overs is given in table 5, and it will be seen that crossveinless flies are found in many different flies homozygous or hemizygous for the *sc ct* section which contains the $+^{cv}$ locus. The crossveinless effect of the H 26 X chromosome therefore cannot be restricted to this neighborhood.

TABLE 5. *Frequencies of crossveinless in various classes, from sc ct v f car/high line* ♀ × *sc ct v f car* ♂

	non-cvl	cvl	% cvl
sc ct v f car	100	0	0
+ + + + +	277	130	32
sc	106	44	29
ct v f car	38	0	0
sc ct	19	2	10
v f car	82	6	7
sc ct v	30	6	17
f car	94	3	3
sc ct v f	9	1	10
car	38	10	21

DISCUSSION

In the experiment described above, selection for the ability to respond to an environmental stimulus has built a strain in which the abnormal phenotype comes to be produced in the absence of any abnormal environment. The crossveinless condition appeared in the foundation stock only as an "acquired character," in the conventional sense. This does not, of course, mean that it was quite independent of the environment; such a supposition would be meaningless, since all development involves not only the genotype but also an appropriate milieu (see Begg, 1952; Waddington, 1952b). What is implied is that crossveinless flies only appeared when the original stock was subjected to some particular abnormal environment, in this case one involving a high temperature at a certain pupal age. In the "high lines" derived from the upward selected stock, however, the crossveinless character appeared in the normal environment which did not involve such a temperature treatment. It has become a hereditary character as contrasted with an acquired one.

This has certainly not happened solely through the selection of a chance mutation which happens to mimic the original acquired character. The genetic basis which is eventually built up for crossveinlessness

differs from the genotype of the foundation stock in several genes. There is evidence of polygenic segregation even in crosses between the high and low lines, both derived from the upward selected stock, and there are still more gene differences between the high lines and the downward selected stock.

The experiments which have so far been performed do not give any final information about the origin of these gene differences. It is well known that different stocks differ in the number and kind of phenocopies they yield after a given treatment. It can therefore be taken as almost certain that there is genetic variability, in this respect, available within any normally variable strain, such as the Wild Edinburgh foundation stock. It is undeniable that such variability existed after the first generation of treatment, since response to selection began immediately. It does not appear necessary to look any further for the origin of all the variability involved throughout the whole course of selection. It is, of course, possible to suggest that the high temperature treatment has itself stimulated the occurrence of new mutations tending to cause crossveinlessness, but there are several points to be mentioned in connection with such a hypothesis. In the first place, the polygenic nature of the differences between the strains would imply that many new mutations would be necessary; secondly, the number of individuals in each generation was so large that new mutations could not have been concentrated in the comparatively small number of generations unless each mutation had occurred simultaneously in a fair number of individuals. Finally, it may be pointed out that even if this hypothesis were advanced, it could bring little comfort to those who wish to believe that environmental influences tend to produce hereditary changes in the direction of adaptation. For there is no reason whatever to suppose that the crossveinless phenotype is adaptive to high temperature; it was merely arbitrarily selected, from among the various phenocopies produced, as the one to be artificially selected, and it is probable that the result of the experiment would have been essentially similar if selection had been practised for the "dumpies" or "miniatures" etc. which also occurred. One could therefore at best suppose that the shock treatment increased the production of many different types of mutations, tending to mimic all the relevant phenocopies. But since there are no considerations which force us to postulate the occurrence of any new mutations at all, it does not seem necessary to pursue the argument any further.

It seems quite possible that if a similar selection for crossveinless formation was repeated, perhaps using a different foundation stock, the same phenotypic effect might be produced with quite a different genetic basis. This has been pointed out by Espinasse (1952), who seems to draw the pessimistic conclusion that studies of the genetic constitutions of strains of animals in the process of evolution tell us nothing of any value. It may be true that we shall never be able to predict exactly what will happen to a species during its future evolution, nor deduce, merely from the phenotypes of animals, what the evolution of their genetic constitution has been. But he seems to pay too little attention to the importance of discovering, by means of such studies, the kinds of process which may be involved in evolutionary change, even if we have to rest content with a knowledge of the categories of possible processes instead of a theory capable of detailed predictions.

It seems worthwhile to devote some attention to the probable nature of the processes which have occurred in building up the high crossveinless lines. The experiment described above was carried out in order to test the possibility of a mechanism which had been suggested by general theoretical considerations (Waddington 1942, 1952c). It had been emphasised that the development of the wild type of an animal is normally more or less efficiently canalised; that is to say it is buffered (or provided with feed-back or cybernetic mecha-

nisms) so that approximately the optimum end-result is attained in spite of minor variations, both genetic and environmental in origin, during the process. This canalisation is presumably brought about by natural selection. For this type of selection, Schmalhausen's (1947) phrase "stabilising selection" seems appropriate, but it is as well to distinguish it clearly, as he does not, from natural selection which merely eliminates deviants, which may be called "normalising" selection. The hypothesis which was put forward suggested that if an animal subjected to unusual environmental conditions develops some abnormal phenotype which is advantageous under those circumstances, selection will not merely increase the frequency with which this favorable result occurs, but will also tend to stabilise the formation of it, and the new development may become so strongly canalised that it continues to occur even when the environment returns to normal. For a series of events of this kind, the name "genetic assimilation" may be suggested. A somewhat fuller discussion of the theory of the process has been given in Waddington (1952d).

The evidence given above is fully in accordance with the predictions of this hypothesis, and, in the absence of any reasons to the contrary, we may regard the production of high crossveinless lines as examples of genetic assimilation by means of the mechanism suggested. In the earlier discussions, the possibility has been raised that the genetic constitution of such an assimilated character may be analysable into two parts, one of which would determine the new epigenetic pathway, while the other, which might be monogenic, would act as a substitute for the original environmental stimulus in switching development into it. In the crossveinless case there is rather little evidence of any clean separation of the genotype into these two components. It is true that there seem to be fewer gene differences between the high and low upward selected lines than between the former and the downward lines. Thus it may be argued that all the upward lines have a certain genetic background in common, which determines a relatively canalized pathway leading to the crossveinless phenotype, while the high lines have in addition a switch mechanism which pushes development over some threshold into this pathway. But if so the switch mechanism still seems to involve more than a single gene, and the distinction between it and the canalising part of the genotype is not clear cut.

It is not intended here to discuss the importance of the genetic assimilation of acquired characters for the general theory of evolution; a few remarks on this have been made elsewhere (Waddington, 1952d, e).

Summary

1. A wild Edinburgh strain of *D. melanogaster* produced no flies showing a break in the posterior crossvein when bred at 25° C., but a certain number occurred (as phenocopies) when the pupae aged 21–23 hours were subjected to 40° C. for four hours.

2. Selection was practised for and against the appearance of the phenocopy, and rapid progress occurred in both directions. After about 14 generations of selection, some flies in the upward selected strain were found to show the effect even when not exposed to the heat shock. From these, lines were built up which threw a high proportion of crossveinless individuals when kept continuously at 25° C. (and even more at 18° C.).

3. The crossveinless character, originally a typical "acquired character," has become incorporated into the genetic make up of the selected races. A process of "genetic assimilation" is described by which this might be supposed to happen; it depends on the tendency of selection not merely to increase the frequency of any favorable character, but also to stabilise its development. A similar suggestion has been advanced by Schmalhausen (1947).

4. The genetic basis of the assimilated crossveinless character is polygenic. There is little evidence of any definite distinction between canalising and switch genes.

Acknowledgment

I should like to express my gratitude for financial support from the Agricultural Research Council.

Literature Cited

Begg, M. 1952. Selection for the genetic basis of an acquired character. Nature, **169**, 625.

Espinasse, P. G. 1952. Selection for the genetic basis of an acquired character. Nature, **170**, 71.

Schmalhausen, I. I. 1947. Factors of evolution, Blakiston, Philadelphia.

Simpson, C. C. 1947. Factors of evolution (review). J. Hered., **40**, 322.

Waddington, C. H. 1940. Organisers and genes, Cambridge Univ. Press.

——. 1942. Canalisation of development and the inheritance of acquired characters. Nature, **150**, 563.

——. 1952a. Selection for the genetic basis of an acquired character. Nature, **169**, 278.

——. 1952b. Selection for the genetic basis of an acquired character. Nature, **169**, 625.

——. 1952c. The evolution of developmental systems. Proc. Australia & N. Z. Assoc. Adv. Sci. (in press).

——. 1952d. Epigenetics and evolution. Symp. Soc. exp. Biol. (in press).

——. 1952e. The evolution of adaptations. Endeavour (in press).

ATYPICAL FORMS OF THE WINGLESS WORKER AND THE WINGED FEMALE IN *MONOMORIUM PHARAONIS* (L.). (*HYMENOPTERA: FORMICIDAE*)

D. W. Hall, B.Sc., F.R.E.S., and I. C. Smith, B.Sc.
Department of Zoology, University of St. Andrews, University College, Dundee

Manuscript received Sept. 29, 1952

Introduction

In ants the existence of forms intermediate between the alate female caste and the apterous worker caste is the basis of suggestions as to the stages in the evolution of the worker.

The species *Monomorium pharaonis* (L.) has been bred in large numbers since 1945 (Peacock & Baxter, 1949) and individuals have appeared, apparently haphazardly, which vary to a greater or lesser extent from the normal types. These atypical individuals are not here described individually because the same degree of modification does not necessarily occur in the head and thorax of the same specimen. A series of head modifications and another of thoracic modifications is presented as having a possible bearing on the evolution of the apterous workers from the alate females.

The general external characters of the typical male, female and worker and the detailed structure of the thorax of *M. pharaonis* (L.) have been considered elsewhere (Hall & Smith, 1951, 1952), in order to establish criteria by means of which atypical forms can be described and interpreted. The characteristics of the head and thorax of the typical castes can be gathered by reference to figures 1–4. A convenient way of expressing head and thorax shape as cephalic and thoracic ratios, by dividing the greatest length by the greatest width (in the former) or the greatest depth (in the latter) (Hall & Smith, 1951, 1952) has shown these ratios for large series *M. pharaonis* to be the following:

Cephalic Ratio (CR): ♀ 0.94, ☿ 0.82
Thoracic Ratio (TR): ♀ 1.8, ☿ 2.7

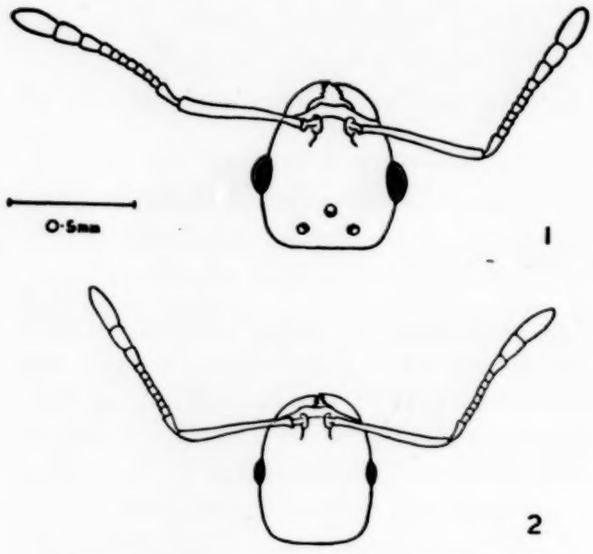
The usefulness of these ratios is readily recognised when intermediate forms from female to worker are considered, as they provide a mathematical expression for the degree of modification which has taken place; *e.g.*, our measurements of the series of intermediate forms of *Pogonomyrmex californicus*, described by Tulloch (1930a) and of *Monomorium rubriceps* (Tulloch, 1930b) show these to have TR's between that of queen and worker. It will be shown that this is clearly indicated also in *M. pharaonis*.

Head Series

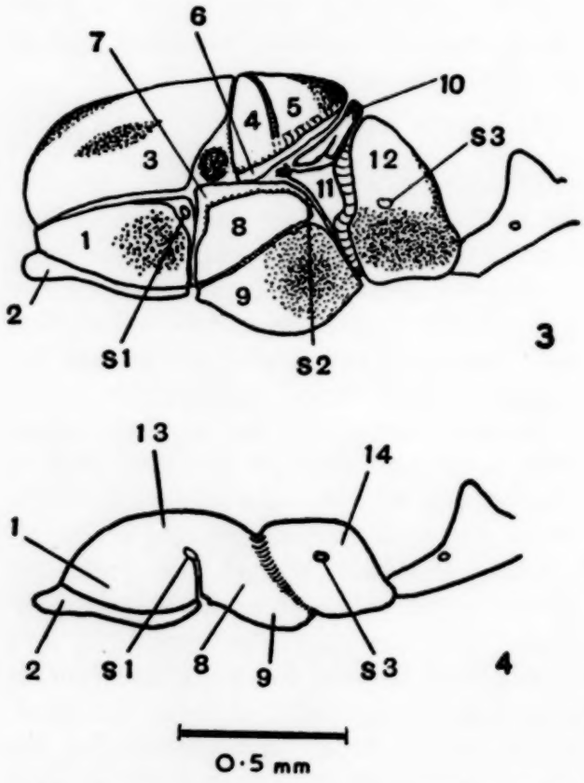
This series of ocellate workers showing uni-ocellate, bi-ocellate and tri-ocellate conditions connects the typical heads of worker and female and is shown in figures 5–9. These figures should be considered with figures 1 and 2 which illustrate the typical heads of female and worker.

A modification of the typical female head is shown in figure 5. This head is distinctly female-like in shape (CR 0.90), in the large compound eyes and in its tri-ocellate condition, though the ocelli are rather smaller than those of a typical female. The corresponding thorax (fig. 11) is still well adapted for wing attachments and from the presence of fore- and hind-wing stumps it can be assumed that the insect concerned had been fully winged, and, as with the typical females (queens), had become dealated shortly after emergence.

The only example we have obtained showing the occurrence of the median ocellus, excepting ergatandromorphs (Hall & Smith, unpublished, is shown in figure 6. This shows a head which is female-like in shape with compound eyes quite



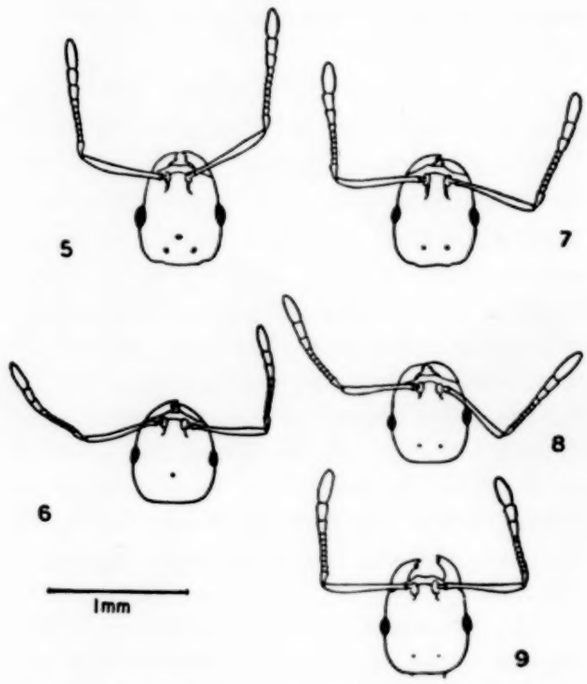
FIGS. 1–2. *Monomorium pharaonis* (L.). Heads of female, (1) and worker (2).



FIGS 3–4. *Monomorium pharaonis* (L.). Thorax, lateral view of female (3) and worker (4). 1, pronotum; 2, prosternum; 3, scutum of mesonotum; 4, prescutellum; 5, scutellum; 6, postscutellum; 7, epimeron of mesothorax; 8, episternite of mesothorax; 9, sternite of mesothorax; 10, mesonotum; 11, epimeron of metathorax; 12, epinotum; 13, mesonotum; 14, metathorax and epinotum. S1, mesothoracic spiracles; S2, metathoracic spiracles; S3, first abdominal spiracles.

considerably smaller than those in the previous example, but possessing only in the median position one small round ocellus. The thorax of this uni-ocellate worker is shown in figure 13.

A further stage towards the typical worker head is obtained by a considerable reduction in size of the compound eyes as shown in figure 7. The head is very slightly female-like in shape (CR 0.85) and two ocelli (the right slightly larger than the left) in the lateral position now



FIGS. 5–9. *Monomorium pharaonis* (L.). Series of heads of atypical workers showing conditions intermediate between the typical female and typical worker.

only remain. This increasing trend towards worker form is also indicated by the corresponding thorax (fig. 14) with its very rudimentary forewings.

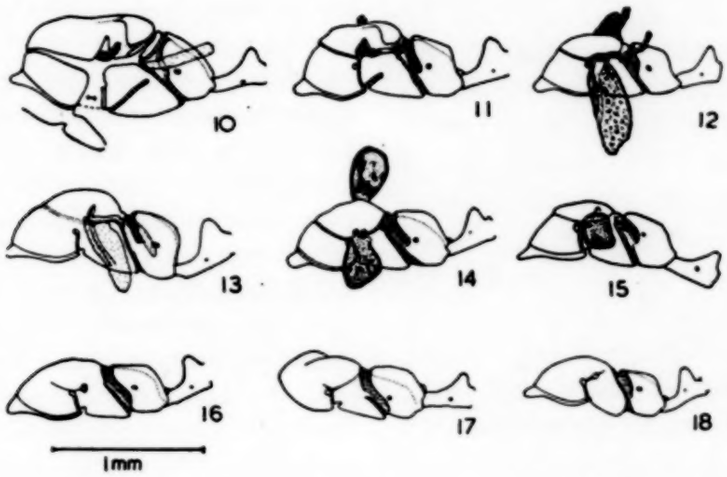
Reduction in size of the lateral members of the dorsal ocelli, as in the head of the bi-ocellate worker shown in figure 8, shows a further stage. The head is now typically worker-like in shape (CR 0.83) and although the ocelli still occupy the normal positions of the dorsal ocelli in the female the compound eyes are worker-type. The corresponding thorax is now

obviously a half-way stage in the development of the worker thorax (see fig. 12).

Minute rudiments of ocelli in the position normally occupied by the lateral members of the dorsal ocelli of the female are the last vestiges of the alate female characters in the worker head (fig. 9). The thorax of this bi-ocellate worker is also very worker-like in composition (see fig. 17).

Thorax Series

The series of figures 10–18 suggests how the fusion of the sclerites and simplification of the typical female thorax to form the simple but highly specialised thorax of the typical worker could have taken place, and illustrates the thoracic modifications in more detail than have similar series for species of *Pogonomyrmex* (Tulloch, 1930a) and *Monomorium* (Tulloch, 1930b). The similarities and points of variance of these and other series are discussed later. The scheme of the typical female thorax (fig. 3) and the typical worker thorax (fig. 4) should be referred to in order to trace the succession of changes.



Figs. 10–18. *Monomorium pharaonis* (L.). Thorax series of forms intermediate between female and worker, lateral view. (A tear is present in specimen fig. 10 between the pronotum and episternite.)

A consideration of these figures leads one to believe that the modification of the female thorax is brought about by the transformation of sutures into furrows, followed by the loss of the furrows causing the coalescence and the subsequent alteration in size and shape of plates.

Sutures: The first suture to disappear is that between the scutum and the prescutellum, causing a partial fusion of these two plates. The sutures between the mesopleuron and epimeron, and the epimeron and metanotum become replaced by broad furrows, while the suture between the metanotum and postscutellum disappears. The last suture to be deleted is that which delimits the mesonotum.

Furrows: The furrows first to disappear are those between the episternite and sternite, and the postscutellum and scutellum, resulting in a coalescence of these plates. There occurs a fusion of furrows in the region of the scutellum, epinotum and sternite, to form a very broad rugose furrow which exists in the worker thorax and divides it into two general regions.

The gradual change in general shape from that of the typical female thorax to that of the worker thorax is illustrated by a consideration of the "thoracic ratio" value for each thorax in the series. Since the TR value for the typical female thorax is 1.8 and that for the typical worker thorax is 2.7, we would expect to find

TABLE 1. *Measurements of the thorax showing the calculated "thoracic ratio" for forms intermediate between female and worker of* M. pharaonis
Magnification about 70 times.—
Arbitrary units of length.

Specimen shown in figure no.	Greatest length	Greatest depth	$\frac{\text{Length}}{\text{Depth}}$ = TR
10	86	48	1.8
11	76	38	2.0
12	72	32	2.2
13	68	28	2.4
14	70	30	2.3
15	70	26	2.7
16	68	25	2.7
17	68	25	2.7
18	61	22	2.8

some TR values between 1.8 and 2.7, depending on the increase in depth which has occurred through modification in the structure of the sclerites. The general shapes illustrated in figures 10–18 would suggest intermediates between worker and female and this is borne out by the fact that the TR's of these specimens (table 1) have a mean of 2.4, the range being 1.8–2.8. The series is listed in descending order from female to worker to correspond with the arrangement given in figures 10–18 and shows the gradual increase from values near that of the typical female thorax through intermediates (TR's 2.0 and 2.3) such as figures 11 and 14 to that of the typical worker thorax.

The first stage in the modification of the thorax is seen in figure 10 in which some of the plates are now not fully formed. A tear is present in this specimen between the pronotum and episternite. The suture running dorsally from the tegula and base of wing area travels for a short distance only, thus causing the prescutellum to be incompletely differentiated from the scutum. The postscutellum is now much smaller, not extending along the border of the prescutellum where a furrow has disappeared. The diagonal furrow separating the episternite and sternite of the mesothorax now reaches only three quarters of the way across. The epimeron of the metathorax is still sharply demarcated and its position fully determined. The fore-wings were presumably normal and removed by the workers before the specimen was found, while the hind-wing, which is rudimentary, has its base in the suture between the metanotum, epimeron and episternite.

Further modifications in the mesonotal and metanotal regions are indicated in figure 11 (TR 2.0) illustrating a specimen which presumably had been fully winged and later had the wings removed. The scutum is now much smaller in size and is only separated from the now ill-defined prescutellum by a small V-shaped suture rising from the base of the fore-wing area in which lies the tegula. The postscutellum here is practically non-existent while the metanotum and epimeron of the metathorax are very much reduced. The episternite and sternite of the mesothorax are very incompletely divided by a furrow which runs only a short distance from the notch between the pronotum and the mesopleuron. A broad deep furrow running over the dorsum between the metanotum and the epinotum almost joins with the furrow between the mesopleuron and the epinotum.

Differentiation of such plates as the scutum, prescutellum, scutellum, and postscutellum is now impossible (fig. 12; TR 2.2) so that the dorsal aspect of the thorax is composed of the mesonotum. The fore-wings are sac-like, containing one major vein with microchaetae, and, at the base, on the broad suture between the mesonotum and the mesopleuron, there is still a prominent tegula. On the dorsal posterior angle of the mesopleuron the minute metathoracic spiracle can still be seen. The hind-wing is present as a very slender sac which has its base at the apex of the now ill-defined epimeron and the base of the metanotum which is still present.

Alteration in the shape of the thorax now occurs by the mesonotum ceasing to overgrow the underlying pronotum (fig. 13). In this specimen a complete division between the mesonotum and pronotum is adumbrated by a contour, and the pro-

notum is not completely delineated from the mesopleuron by a suture. A sac-like fore-wing is present, which contains a rather thick vein and has its base in a slightly sclerotised area on the ventral surface of the mesonotum. An area of heavier sclerotisation may represent the tegula. A rudimentary hind-wing is present which again has its origin at the apex of an ill-defined epimeron area. The suture between the mesonotum and mesopleuron is narrowing and at the posterior end of it can be seen the last remains of the metanotum.

Further modification now takes place in the region of the wing bases and the metathorax (fig. 14). The fore-wings are present only as expanded sacs heavily chitinised on the periphery, and rising from the very much narrowed suture between the mesonotum and mesopleuron. A very broad rugose furrow is now seen running over the dorsum of the metathorax and joining the furrow between the mesopleuron and the metathoracic epinotum. On this furrow the vestige of the hind-wing is now all that is visible.

A shortening and narrowing of the existing sutures takes place, while the furrows in the epinotal region coalesce (figs. 14 and 15). This is followed by the disappearance of these sutures (figs. 16–18) until only one remains as in the worker thorax (fig. 2).

If we consider the thorax series in the reverse direction (*i.e.*, worker towards alate female) we see that the mesonotum of the worker corresponds to three plates in the female, viz., the scutum, scutellum and prescutellum. Moreover, the postscutellum is apparently formed by a backward projection of this prescutellar plate, the two being separated in the typical female thorax by a shallow rugose furrow.

Wing Series

The functionless wings shown in figures 12–15 indicate the possible stages in the evolution of aptery. The progressive reduction in size of the thorax and wings, with the accompanying fusion or simplification of sclerites, may represent retrogressive evolutionary stages.

Fore-wings are present as wing sacs of approximately the normal shape but with indistinct veining, except in the case of a definite sub-costa (figs. 12 and 13); the hind-wings are veinless wing sacs. A step nearer aptery is indicated by the wings shown in figures 14 and 15. The shape of these fore-wings bears no resemblance to that of the perfect wing and they are exceptionally interesting in that they show areas which appear to be quite heavily chitinised. These areas do not resemble the structure of veins, but may well be the forerunners of such. A minute, veinless, sac-like vestige, very similar in appearance to the stub of a broken wing (see fore-wing, fig. 10) might represent the stage preceding total aptery and could therefore be phylogenetically the most recent condition. The suggestion of a region of wing origin in the hind-wing position (fig. 15) obviously represents a further and final step in the loss of wings.

Discussion

In the Myrmicinae several cases have been described of abnormal or atypical ants being found in natural nests, *e.g.*, in *Leptothorax emersoni* Wheeler, eleven different types of female individuals were distinguishable by external characters and included queen, micrygyne, ergatoid, ocellate workers, macroergates and microergates (Holliday, 1904). In the genus *Monomorium* cases are known where the females have a thoracic structure typical of winged forms, yet they show no indication of ever having borne wings (Wheeler, 1905a). This type of aptery, unaccompanied by the usual fusion of sclerites and by marked diminution in the size of the thorax, was observed in *Monomorium floricole* Jerdon, *M. carbonarium* F. Smith sub sp. *ebeninum* Forel and *M. minutum* Mayr. sub sp. *ergatogyna*. Both winged and ergatoid females have been described in *M. andrei* while the ergatoid character of the female occurs in *M. shurri* and *M. dichroum* (Wheeler, 1905a). Differences

in the size of thorax and wings in the females of *M. rothsteini* and *M. subapterum* exist, the condition of subaptery in *M. subapterum* being normal, while in a nest of *M. rubriceps* intermediate stages between the alate and apterous condition have been described (Tulloch, 1930b). Gradational changes in the wing structure have also been figured in species of *Monomorium* (Wheeler, 1917). A nest of *Pogonomyrmex californicus* Buckley was discovered in which there were a number of workers with wing vestiges (Tulloch, 1930a).

The thorax series described for *M. pharaonis* differs from other series described, *e.g.*, those on *Pogonomyrmex californicus* (Tulloch, 1930a), *Monomorium rubriceps* (Tulloch, 1930b), and *Leptothorax emersoni* (Holliday, 1904). First, it will be seen that our series is composed of specimens occurring haphazardly and infrequently in a number of colonies, a point of major difference from that described for *Pogonomyrmex* (Tulloch, 1930a) where the complete series was taken from a single nest. Secondly, in most of the intermediate forms of *M. pharaonis* vestigial wings (both fore- and hind-wings) are present, while in the other series there is almost a complete gap between the perfect winged condition and the wingless condition on an almost perfect worker thorax. In the modification of the *Monomorium* thorax given by Tulloch (1930b) there is only one individual figured with very rudimentary wings, stumps of the fore-wings being present. Wheeler (1905b) has described a number of worker ants of *Myrmica rubra scabrinodis* var. *schenki* Emery with vestiges of anterior wings, these individuals being perfectly normal workers in every other respect (pterergates). This suggests that worker ants must once have possessed functional wings and the wingless condition has been acquired during phylogeny. Our close investigation of the thorax series in *M. pharaonis* also indicates the origin of the scutum, the scutellum, the prescutellum, and the postscutellum.

Kalmus (1945) has attempted to show that there is close correlation between wings and ocelli in insects in general. That there is some correlation is certain and our results bear this out. An upset in the one is usually linked in some degree to an upset in the other but our results show that the correlation is not close (cf. figs. 5 and 11, 6 and 13, 8 and 12, 9 and 17). Experimental evidence is therefore needed to decide whether such a time/growth relationship is really coincidental as might well be the case, or whether there is in fact coordination between ocellus and wing development in normal ontogeny.

The topic "Origin of Castes" has always been controversial among myrmecologists: have the various forms been produced by continuous or discontinuous variation or by nutritional factors?

The appearance of intermediate forms could have an orthodox explanation, that of discontinuous variation or mutation, which is embodied in the blastogenic interpretation. From a mutant female a form with functionless wings could arise and this form, assuming it was capable of reproduction, by further mutation would give the ergatoid female. This process of modification by chromosomal or genic change would only account for the formation of the apterous condition through the stages shown in figures 10–18, if we assume that each stage was capable of reproduction and of passing on the mutated condition further down the line. Dissection of a few workers has revealed rudimentary ovaries but our observations on forms intermediate between female and worker do not allow us to state whether these individuals were capable of producing eggs. Only after consideration of the gonad condition could further speculation on these lines proceed. This aspect we hope to investigate. The work of Holliday (1904) is interesting in this respect for she found that all the eleven types of female individuals studied, from "queen" to micrergate, possessed well-developed ovaries containing mature eggs, and all but two individuals possessed the receptaculum seminis. Further, during physiological studies a

large number of ergatogynes in several families were examined and a large percentage of functional ovaries and a receptaculum seminis were observed. Since intermediate forms can possess functional ovaries, it would therefore appear that the apterous condition could have been brought about by mutation. Is it possible that the apterous condition has taken an orthogenetic course (not one of ortho-selection) where the final result is of a distinctly beneficial nature? This of course would mean mutation occurring repeatedly in a given direction, a conclusion which could be supported by such experimental results as heat-produced mutations in *Drosophila* (Jollos, 1930).

That nutritional factors are of significance in the origin of castes in ants has long been suspected. We know that in bisexual species of Hymenoptera males are haploid and females diploid (for reference see Sanderson, 1932) and it can be stated that this condition holds for *M. pharaonis* (unpublished work by one of the present authors, I.C.S.). Further, from facts established in the case of the honey bee (for references see Sanderson and Hall, 1951) it might reasonably be supposed that the different female castes in ants are produced by special feeding, and as will be seen, our observations on *M. pharaonis* lend support to this view.

In *M. pharaonis* the distinction between the sexuals and workers can be first observed in the larval stage (Peacock, A. D., and Baxter, A. T., 1950). During the 9–10 days after eclosion the young larvae, both sexual and worker, show golden-yellow gut contents, when liver and sugar granules are available as food. (The gut content color is very pale yellow when the food is sugar alone or rabbit flesh alone.) At this stage the worker larvae are about half grown and have presumably obtained the same kind of food as the larvae destined to be sexuals. From this point onwards, however, until the worker prepupal stage (*i.e.*, after another 7–8 days) the gut content darkens, becoming brown then black when liver is the food. The circumstances of the darkening (with liver) are as follows: when the larva is 9–10 days old the gut content is golden yellow, when 12–14 days old the color is brown, and when 15–16 days old there is a rapid change to black. A black faecal mass (the meconium) finally leaves the larval gut just before the formation of the prepupa about the 17th day of larval life, the adult workers helping considerably in the extraction of the mass. When liver is not included in the diet the meconium is yellow-brown in color. A similar sequence of vents regarding darkening in color can be observed with the sexual larvae but the timing is different. The sexual larvae after the first 8–10 days continue to show a golden-yellow gut content, and it is not until they are 14–17 days old (when they are distinguishable from worker larvae by their larger size and slightly different shape) that the gut content commences to darken, the rapid change to black occurring when 19–20 days old.

There is then a nutritional difference between worker and sexual larvae which is apparent by a darkening of the gut contents, this darkening commencing about the 9th to 11th day in the larval life of a worker, and about the 14th to 17th day in the larval life of a sexual. This colour change could be brought about by (1) the cessation of feeding followed by the gut contents undergoing changes of a digestive nature, or (2) changes in the quality of food given to the larvae by the workers during the last 6–7 days of larval life, or (3) a decrease in the quantity of food given to the larvae by the workers during the last 6–7 days, resulting in the accumulation of waste material forming an ever-increasing percentage of the total gut content. The first possibility does not appear likely since observation shows that worker larvae even 14–16 days old are given food. Regarding the second possibility, the quality of food could be dependent on a difference in the type of food or on the addition of an enzyme to the same food by the adult workers. We have never observed change in the type of food administered, but dif-

ferences of an enzymatic nature, hitherto not investigated, cannot be ruled out. The third possibility, involving quantity of food, is also a matter for investigation. It does, however, provide a simple explanation for the colour change phenomena observed in the gut of the larvae.

As the worker larval period lasts about 17 days while that of the sexuals is about 21 days (Peacock, A. D., and Baxter, A. T., 1950), the difference between worker and sexual seems therefore to be due to food being fed in quantity to the sexual larvae for a further period of six to ten days. The difference between the female and worker castes could then be attributed to quantity of food, as likewise could be the appearance of the intermediate forms. If larvae destined to be workers received an adequate diet of food for the first eleven to fourteen days, instead of eight or nine days, they would then presumably give rise to female-worker intermediates. This possibility is supported by observations that a number of worker-type large larvae and prepupae slightly larger and broader at one end than the normal have occurred in our colonies. Further, in colonies of *M. pharaonis* there is a high egg mortality which increases with the occurrence of sexuals in a colony. This mortality may be due to neglect of the eggs by the workers (a phenomenon observed under certain conditions) or to the eggs being fed to the larvae. It may be that the relationship of number of workers to number of larvae (worker/larva ratio) in a colony conditions the onset of sexual waves. However, these points require much greater investigation. Moreover, the possibility of caste differentiation being a function of the rate of egg deposition (Flanders, 1945) is not supported by data from our artificial colonies. For the foregoing reasons therefore it would appear that the production of female castes has a trophogenic basis.

Brian (1951) takes the view that caste determination in *Myrmica rubra macrogyna* is a modified form of trophogenesis and that intercastes are arrested stages in ontogeny with small evolutionary significance. To support this view he puts forward experimental evidence of intercaste production—imperfect development of the female characters—brought about by interference with the larval food supply. This would fall within the framework suggested by Kalmus (*loc. cit.*) that caste-determination is either basically due to a gene mechanism in individual cells acting after fertilisation, and being modifiable by nutrition; or perhaps, alternatively, to a gene mechanism producing hormonal control in the whole organism. The former is more probable since genic upsets in individual cells could then give rise to phenotypic anomalies such as those frequently found in most species of ants.

Nevertheless, whilst it is true that intercastes do possibly represent ontogenetic stages and that it is improbable that we shall ever know the true evolutionary course of caste-determination in ants, it is difficult to escape from the idea that this evolution must have proceeded by stages involving forms very like those we have described.

Summary

Various types of atypical individuals which have appeared in artificially reared colonies of *Monomorium pharaonis* (L.) over a period of five years are described.

A possible course of the evolution of the worker ant is indicated by two complementary lines of evidence, the first concerned with head structures, and the second with thoracic structures, relating to forms intermediate between female and worker. In considering intermediate forms the application of cephalic and thoracic ratios has been of value. The observations made are discussed in relation to similar series found in other ants and already presented by other investigators.

The wing structures of the series of intermediate forms described indicates the possible stages by which aptery has evolved.

Caste determination in ants is discussed.

In *M. pharaonis* (L.) there is a nutritional difference between larvae destined to be workers and those destined to be sexuals. This is apparent by a darkening of the gut contents, this darkening commencing when the worker larva is 9–11 days old and when the sexual larva is 14–17 days old. Explanations of this darkening phenomenon are discussed. In *M. pharaonis* (L.) it seems probable that caste determination is trophogenic—the difference between worker and sexual seems to be due to generous feeding of the sexual larvae for a further period of 6–10 days.

Acknowledgments

We wish to acknowledge our indebtedness to Professor A. D. Peacock for helpful criticism throughout, and to Mr. A. T. Baxter for co-operation in the experimental and recording work. The work was made possible by a grant from the Bowden Entomological Research Fund of the University of Glasgow. We are grateful to the Ent. mon. Mag. for permission to publish figures 1–4.

Literature Cited

Bhattacharya, G. C. 1942–43. Reproduction and caste determination in aggressive red ants, *Oecophylla smaragdina* Fabr. Trans. Bose Res. Inst., **XV**.

Brian, M. V. 1951. Caste determination in a Myrmicine ant. Experientia, **7**: 5, 182.

Brues, C. T. 1903. The structure and significance of vestigial wings among insects. Biol. Bull., **4**: 179–190.

Cumber, R. A. 1949. The biology of Humble-Bees, with special reference to production of the worker caste. Trans. R. ent. Soc. Lond., 100, **1**: 1–45.

Donisthorpe, H. St. J. K., and B. D. W. Morley. 1945. A list of scientific terms used in myrmecology. Proc. R. ent. Soc. Lond., (A), **20**.

Flanders, S. E. 1945. Is caste differentiation in ants a function of the rate of egg deposition. Science, **101**: 245–246.

Hall, D. W., and I. C. Smith. 1951. Studies in Pharaoh's Ant, *Monomorium pharaonis* (L.). Pt. 6. External characters, size and cephalic ratio. Ent. mon. Mag., **87**: 217–221.

——. 1952. Studies in Pharaoh's Ant, *Monomorium pharaonis* (L.). Pt. 7. Thoracic structures, typical and atypical. Ent. mon. Mag., **88**, 97–102.

Holliday, M. 1904. A study of some ergatogyne ants. Zool. Jb. (Syst.), **19**: 293–328.

Jollos, V. 1930. Studien zum Evolutionsproblem I. Biol. Cent., **50**: 541–554.

Kalmus, H. 1945. Correlations between flight and vision and partly between wings and ocelli in insects. Proc. R. ent. Soc. Lond. (A) **20**: Pts. 7–9, 84–96.

Peacock, A. D., and A. T. Baxter. 1949. Studies in Pharaoh's Ant, *Monomorium pharaonis* (L.), Pt. 1. The rearing of artificial colonies. Ent. Mon. Mag., **85**: 256–60.

——. 1950. Studies in Pharaoh's Ant, *Monomorium pharaonis* (L.). Pt. 3. Life history. Ent. mon. Mag., **86**: 171–178.

Reid, J. A. 1941. The thorax of the wingless and short-winged Hymenoptera. Trans. R. ent Soc. Lond., **91**: 8, 367–446.

Sanderson, A. R. 1932. The cytology of parthenogenesis in Tenthredinidae. Genetica, **14**.

Sanderson, A. R., and D. W. Hall. 1951. Sex problems in the Honey-Bee. Endeavour, **10**: 37, 33–39.

Tulloch, G. S. 1930a. An unusual nest of *Pogonomyrmex*. Psyche, **37**: 61.

——. 1930b. Thoracic modifications accompanying the development of subaptery and aptery in the genus *Monomorium*. Psyche, **37**: 202–206.

——. 1935. Morphological studies of the thorax of the ant. Ent. Amer., **15**, 3: 93–130.

Wheeler, W. M. 1905a. The ants of the Bahamas. Bull. Amer. Mus. Nat. Hist., **21**: 79–135.

——. 1905b. Worker ants with vestiges of wings. Bull. Amer. Mus. Nat. Hist., **21**: 405–408.

——. 1910. Ants. Columbia Univ. Press.

——. 1917. The phylogenetic development of subapterous and apterous castes in the Formicidae. Proc. Nat. Acad. Sci., **3**: 109–117.

——. 1937. Mosaics and other anomalies among ants. Cambridge, Mass.

Whiting, P. W. 1945. Quart. Rev. Biol., **20**: 3, 231–260.

EXPERIMENTAL BACKGROUND TO THE STUDY OF THE DISTRIBUTION AND ABUNDANCE OF INSECTS

III. The relation between innate capacity for increase and survival of different species of beetles living together on the same food [1]

L. C. BIRCH

Zoology Department, University of Sydney

Received January 30, 1953

INTRODUCTION

When any one of the three beetles *Rhizopertha dominica* Fab., the small strain and the large of *Calandra oryzae* L., was allowed to increase in numbers in a limited space in which the amount of food was kept constant, the maximum numbers which the populations attained were correlated with the innate capacity for increase (or the intrinsic rate of increase r) (Birch, 1953b).

In this paper we shall examine whether there is a relationship between the numbers of these beetles and their innate capacity for increase when two species occur together in the one population. The experimental models which were set up are similar to those described in an earlier paper (Birch, 1953b) in which single species multiplied in amounts of grain which were kept constant, except that in the present experiments each tube of grain contained two species; an adult male and female of each species were placed in each tube at the beginning. Combinations of temperature, moisture and food were chosen so that in some experiments one species had a higher innate capacity for increase than the other whilst in other experiments this same species had a lower innate capacity for increase than the other. The appropriate information for planning the experiments in this way was obtained from a previous paper (Birch, 1953a).

This latter aspect constitutes the novel feature of these experiments. Other workers have done experiments in which two or more species utilise the same resources of space and food, but so far as I am aware these experiments have not been designed to investigate the possible relationship between the innate capacity for increase and the trend in numbers of each species.

Studies of this sort are commonly referred to as "inter-species competition." I have decided to avoid using this phrase because there are a number of respects in which the concept of competition does not apply to experimental models of this sort. Ecologists use the concept of competition in a number of ways. Sometimes they include predation as an aspect of competition. In other cases it is used loosely to cover all "struggles" which the organism may have with its environment. But the advantages possessed by some species in the "struggle for existence" have no connection with competition. Darwin made this quite clear in the third chapter of the Origin of Species. Another unfortunate aspect of the use of the concept of competition is the implication of emotion or purpose and because of this Dobzhansky (1950) has suggested that it is best avoided in discussions of the causes of evolution. This is equally sound advice for ecology. Ecologists have not been unaware of the confusion in the use of the concept of competition. Thompson (1939) drew attention to some of its undesirable implications in ecology and Ullyett (1951) has questioned its appropriateness as applied to the relation between two or more species of blowflies which feed on the same food without directly interfering with one another. If the maggots are numerous

[1] This work was aided with a research grant from the Commonwealth Research Grant to the University of Sydney.

there may not be enough food to go round and only a few of them get enough food to survive. Ullyett compared this situation to the slums of a large city where families are usually large even though food is scarce. He wrote "it can hardly be said that the children in the families 'compete' for the available food. Yet they suffer from the shortage very much in the same way as do the overcrowded progeny of the blowflies."

Amongst these and other uses of competition we might choose to select its literal meaning which is "together seek," but this would still invite confusion when others continue to use it in a broad and largely metaphorical sense. I shall, instead, avoid its use altogether and consider the experimental models described in this paper with respect to what happens to the numbers of two species when they together utilise the same resources which are in limited supply.

Design of Experiments

Each experimental model consisted initially of 12 grams of grain with a pair of newly emerged adults of each of two species of beetles. They were kept in 4″ × 1″ vials covered at one end with phosphor-bronze gauze. The vials were kept at constant temperatures (±0.1° C.) and constant humidities and the adults were counted at monthly intervals except for the first 8 weeks when they were counted at 2 weekly intervals. The grain was sifted and made up to 12 grams at two weekly intervals. At the same time control experiments were done in which single species were kept under the same conditions. The control experiments have been described in detail in a previous paper (Birch, 1953b). The general routine of sifting used in all these experiments was described in this earlier paper and need not be repeated here. It was, of course, necessary to separate the species each time they were counted. This presented some difficulties in the case of the large and small strains of *C. oryzae*. These beetles were separated on size but since there is an overlap in size of the two species it was never possible to make a completely reliable separation. Between 5 and 10 per cent of the population fell in the overlapping size group and these were arbitrarily allotted to the two species in equal numbers.

The routine of sifting, counting and replacing food was continued until one of the species eventually became extinct, this took about two years in most of the experiments. This applied to all experiments except those shown in figure 3. These

Table 1. *Showing the four series of experiments in which populations of two species were grown together with a constant amount of grain*

Experiment	Species	Grain	Temp., ° C.	Moisture content of grain per cent	Innate capacity for increase*	
					r	λ
1	*C. oryzae* (small strain)	Maize	29.1	13	0.417	1.52
	C. oryzae (large strain)	Maize	29.1	13	0.436	1.55
2	*C. oryzae* (small strain)	Wheat	29.1	14	0.772	2.15
	C. oryzae (large strain)	Wheat	29.1	14	0.564	1.76
3	*C. oryzae* (small strain)	Wheat	29.1	14	0.772	2.15
	R. dominica	Wheat	29.1	14	0.578	1.78
4	*C. oryzae* (small strain)	Wheat	32.3	14	0.501	1.65
	R. dominica	Wheat	32.3	14	0.686	1.99

* From Birch (1953a); r and λ are alternative expressions for the innate capacity for increase; r is the infinitesimal rate of increase and λ is the finite rate of increase (number per female per week).

TABLE 2. *Showing the variability in the experiments. The figures in the body of the table are mean values for the coefficient of variabilities of monthly observations, each figure is the mean of four monthly values*

	Experiment 1. 29.1° C. Maize		Experiment 2. 29.1° C. Wheat		Experiment 3. 29.1° C. Wheat		Experiment 4. 32.3° C. Wheat	
Weeks	*C. oryzae* (small)	*C. oryzae* (large)	*C. oryzae* (small)	*C. oryzae* (large)	*R. dominica*	*C. oryzae* (small)	*R. dominica*	*C. oryzae* (small)
6– 10	53.1	47.4	32.4	52.4	57.1	22.2	21.8	78.5
10– 26	62.6	32.5	21.4	54.6	44.0	28.6	18.3	81.2
26– 42	57.6	36.1	29.4	71.2	94.7	31.1	21.1	82.3
42– 58	69.4	43.3	43.3	66.3	70.8	27.6		
58– 74	71.5	33.1	19.8	99.1	66.6	22.7		
74 –90	94.7	17.4	23.85	72.6	76.8	19.7		
90–106	89.7	13.5			37.5	19.6		
106–122	43.4	18.7			55.0	16.3		
122–138	19.6	8.4			80.0	21.0		
138–154	38.2	12.1			38.3	14.2		
154–170					52.8	13.0		
170–186					63.1	8.7		

were terminated after four years, though at the end of that time some replicates still contained two species.

Four series of experiments referred to as experiments 1–4 were done, these are shown in table 1. Each series was replicated 15 times. In experiment 1 the large strain of *C. oryzae* had a slightly higher innate capacity for increase than the small strain. The reverse relationship held in Experiment 2. In Experiment 3 the small strain of *C. oryzae* had a higher innate capacity for increase than *R. dominica*. The reverse case is shown in Experiment 4. There are thus two sorts of experiments; in the one, species A had the advantage and in the other, species B had the advantage.

THE TREND IN NUMBERS IN THE EXPERIMENTAL MODELS

The trend in numbers in the four series of experiments are shown in figures 1–4. The results from different replicates were

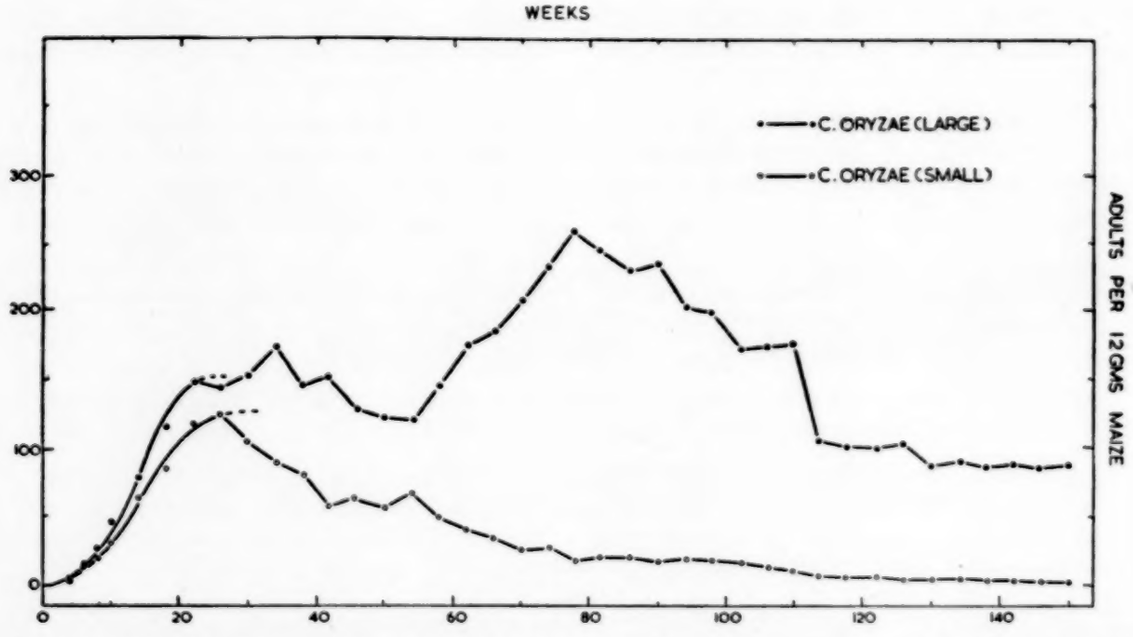


FIG. 1. The trend in numbers of adults of the small and large strains of *C. oryzae* living together in maize of 13 per cent moisture content at 29.1° C. The smooth curves are calculated logistic curves.

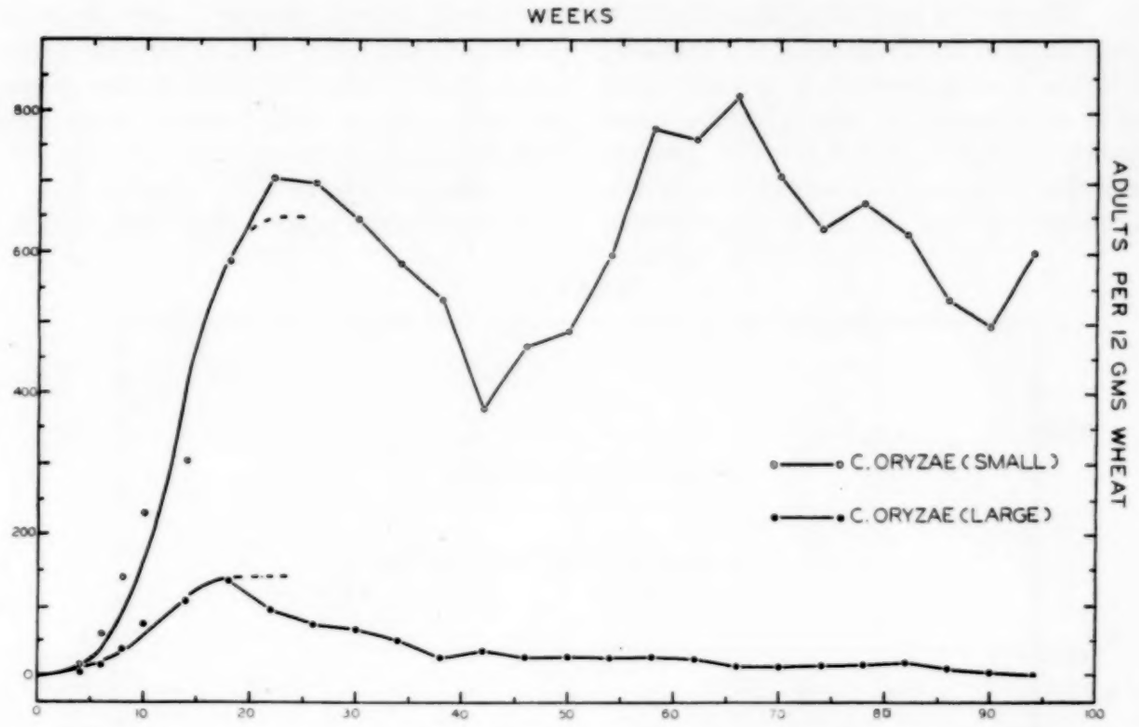


FIG. 2. The trend in numbers of adults of the small and large strains of *C. oryzae* living together in wheat of 14 per cent moisture content at 29.1° C. The smooth curves are calculated logistic curves.

surprisingly uniform. The full tables of results are so extensive that they are not shown. Instead a summary of variability is provided in table 2. The coefficients of variability of 250 means were calculated. These were then arranged in groups of

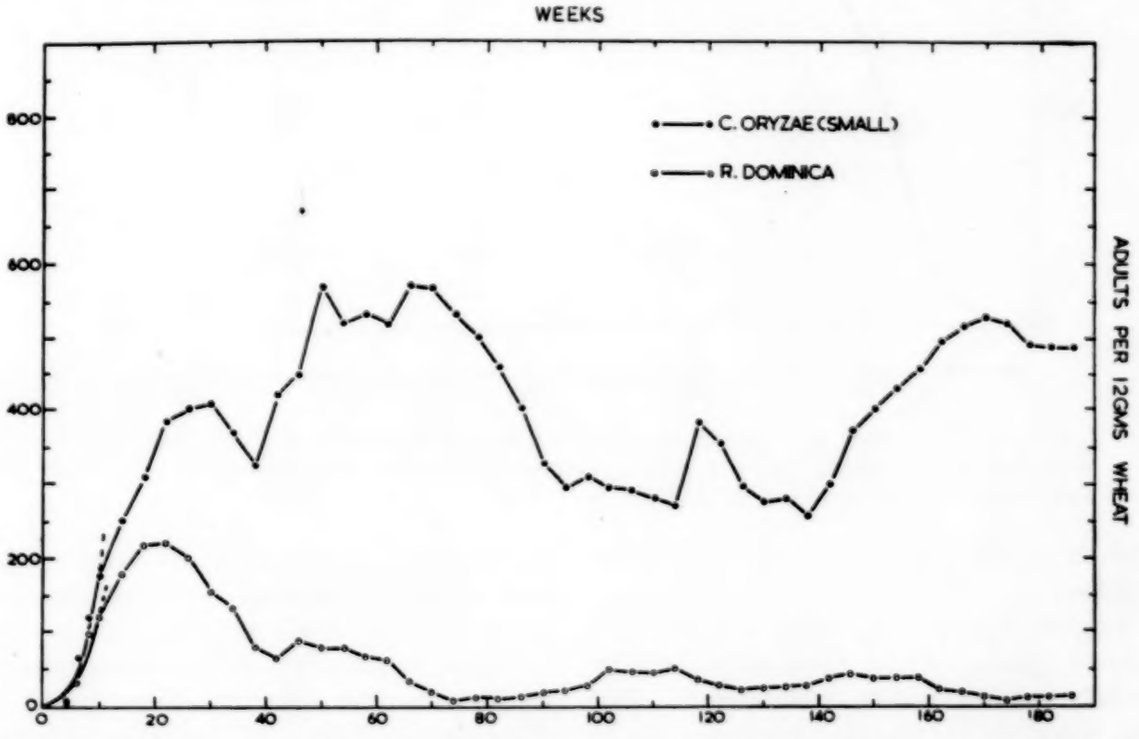


FIG. 3. The trend in numbers of adults of the small strain of *C. oryzae* and *R. dominica* living together in wheat of 14 per cent moisture content at 29.1° C. The smooth curves are calculated logistic curves.

four. The means of these groups of 4 are shown in table 2. In general the variability in these experiments is greater than that in experiments in which species grew separately (Birch, 1953b). The greater variability occurs in the means for the unsuccessful species in each experiment.

smoothed curves through the observed points during the initial growth phase (figs. 1–4). The formulae of the curves are not given as they have no theoretical significance in these experiments.

A comparison between figures 1–4 in this paper and figures 1–4 (Birch, 1953b)

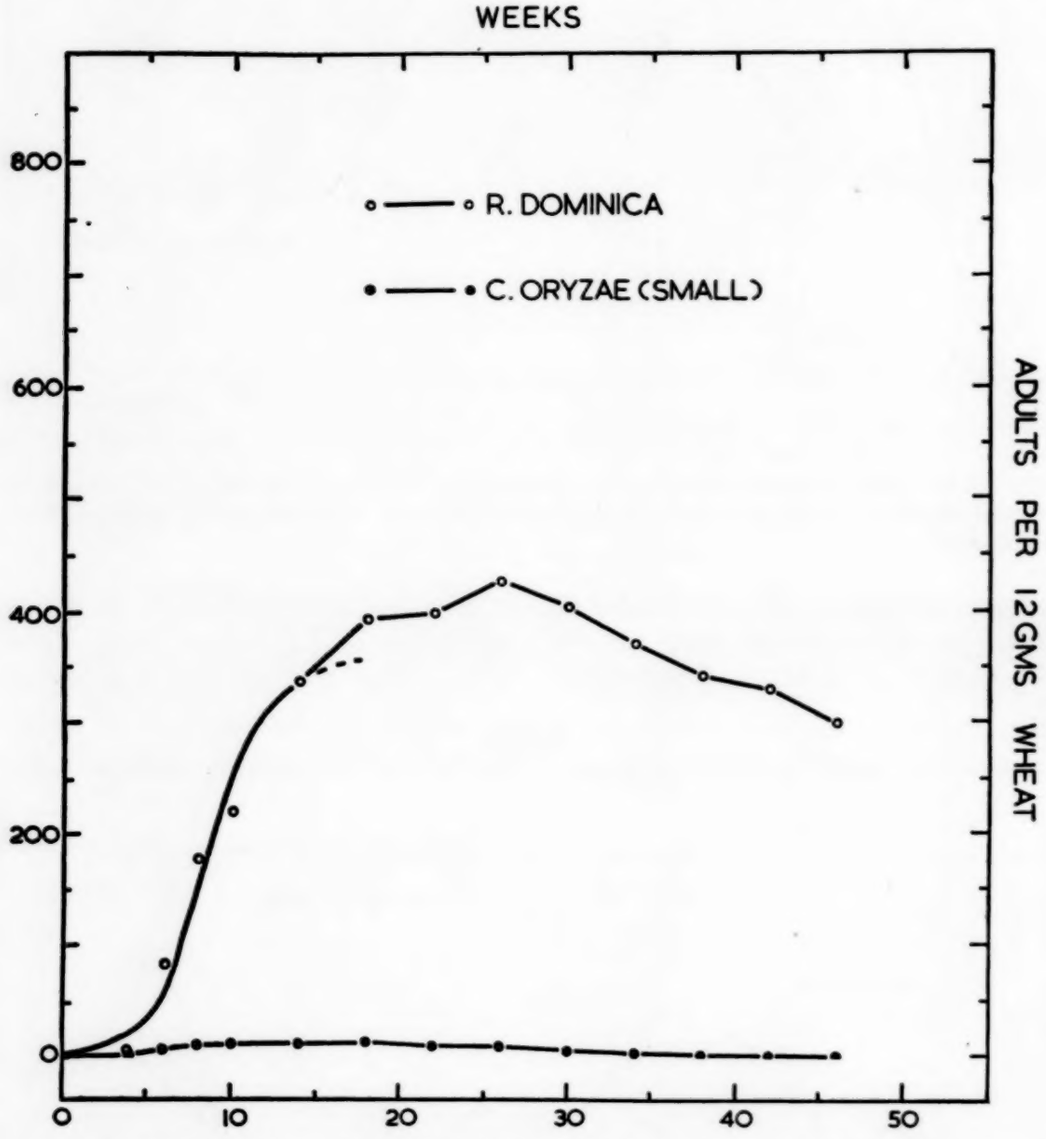


FIG. 4. The trend in numbers of adults of the small strain of *C. oryzae* and *R. dominica* living together in wheat of 14 per cent moisture content at 32.3° C. The smooth curves are calculated logistic curves.

This was the species present in smaller numbers.

Logistic curves were fitted to the initial growth phase of the populations where density was increasing continuously. But this was done for no other purpose than to provide a convenient means of drawing the

shows quite clearly that the numbers of each species when they occurred together were less than their numbers when they occurred separately. And in each experiment, with the provisional exception of Experiment 3 (fig. 3), one species eventually became extinct in each replicate. In

TABLE 3. *Showing the relation between the innate capacity for increase (r) and survival when two species together utilise the same food and space*

Experiment	Species	Grain	Temp., °C.	Moisture content, %	Innate capacity for increase (r)				Surviving species	Number of weeks for unsuccessful species to become extinct	
					R. dominica (R)	*C. oryzae* (small) (C_s)	*C. oryzae* (large) (C_l)	Ratios		Mean	Range
1. (Fig. 1)	*C. oryzae* (small strain) and *C. oryzae* (large strain)	Maize	29.1	13	—	0.417	0.436	$C_l > C_s$	C_l	100	74–150
2. (Fig. 2)	*C. oryzae* (small strain) and *C. oryzae* (large strain)	Wheat	29.1	14	—	0.772	0.564	$C_s > C_l$	C_s	69	46– 95
3. (Fig. 3)	*C. oryzae* (small strain) and *R. dominica*	Wheat	29.1	14	0.578	0.772	—	$C_s > R$	C_s	—	38–190+
4. (Fig. 4)	*C. oryzae* (small strain) and *R. dominica*	Wheat	32.3	14	0.686	0.501	—	$R > C_s$	R	37	26– 47

Experiment 3 (fig. 3) *R. dominica* became extinct in 7 out of the 15 replicates by the 190th week and the numbers of *R. dominica* were very low in the remaining replicates. The experiment had to be terminated at the 190th week.

The species which became extinct was always the same in each of the 15 replicates of a series, though there was a wide variation in the time for this to take place in the replicates within a series (see table 3, last two columns). In each of the series the successful species was the one with the higher innate capacity for increase (table 3). Park (1948) did experiments with comparable numbers of replicates with *Tribolium confusum* and *T. castaneum* and in his experiments one species always became extinct, but this was not always the same species in each replicate in a series.

Whereas the large strain of *C. oryzae* survived in maize (fig. 1), the small strain was the survivor in wheat (fig. 2). The large strain had a higher innate capacity for increase than the small strain in maize but the reverse held in wheat. The small strain succeeded in wheat at 29.1° C. when it occurred with *R. dominica* (fig. 3). But the reverse held when the temperature was 3.2° higher and the innate capacity for increase of *R. dominica* was higher than that of *C. oryzae* (fig. 4). A comparison of figures 3 and 4 shows that the curves of the two species are not only reversed in their positions but at the higher temperature *C. oryzae* scarcely makes up any appreciable proportion of the population at any stage, despite its large numbers in the control populations at the same temperature (see fig. 4, Birch, 1953b). When *R. dominica* was given an initial advantage over *C. oryzae* its depressing effect on the rate of increase of *C. oryzae* was greater than the depressing effect of *C. oryzae* on *R. dominica* when the former species had the initial advantage.

Not only was there a wide variation in the time taken for one species to become extinct in the different replicates within a series but there was also a big difference between the mean time for extinction of a species for different series (table 3). The differences do not appear to be related to the size of the differences between the innate capacities for increase of the two species occurring together.

Discussion

Perhaps the most important feature of the experiments described in this paper is the demonstration that the successful one of two species which together utilise the same resources of space and food depends upon its higher innate capacity for increase. The outcome of these experiments can thus be predicted on the basis of characteristics which the species exhibit when they are living alone. Such a complete correlation between the inate capacity for increase and success in survival would not be expected in other experimental models in which the success of a species may be largely dependent upon its direct interference with the rate of increase of the other species in ways which could not be predicted from a study of the species living alone (*e.g.*, Birch, Park, and Frank, 1951).

These experiments with *Calandra* and *Rhizopertha* demonstrate quite clearly that the species which is successful in one set of conditions can be made the unsuccessful species in another set of conditions when these give it a reduced innate capacity for increase. Thus when the temperature was 29.1° C. *C. oryzae* dominated *R. dominica* but when the temperature was raised to 32.3° C. *R. dominica* dominated *C. oryzae*. Both species increased rapidly at these temperatures when they occurred separately but *C. oryzae* had a higher value for r at the lower temperature and *R. dominica* had the higher value at the higher temperature. Moore (1952a) obtained a reversal in the success of one species of *Drosophila* as compared with another in this same sort of way; at 25° C. *D. melanogaster* was the successful species but at 15° C. *D. simulans* was the successful species. Moore did not investigate the relative innate capacities for increase of the two species and so it is not possible to state if this

experimental model was similar in other respects to the experimental models described in this paper. Park (1948) demonstrated a reversal in the final equilibrium between the flour beetles *T. confusum* and *T. castaneum;* when the Sporozoan parasite *Adelina* was present *T. confusum* was usually the successful species, the results were reversed when *Adelina* was excluded from his experiments.

The results of experiments with *Rhizopertha* and *Calandra* and Moore's (1952a) experiments with *Drosophila* suggest that there might be one temperature at which two species would be equally favored and at which they might therefore exist together indefinitely. The improbability of this being so can be illustrated by considering some theoretical models. If we suppose that two species are initially present in equal numbers the proportional effect of density is the same for each species, then the following conditions would have to be fulfilled if they were to be equally favored at one particular temperature:

1. If the proportional inhibition of species A by species B was the same as the proportional inhibition of species B by species A then the appropriate temperature would be given when the innate capacities for increase were the same.

2. If the proportional inhibition of species A by species B was different from the proportional inhibition of species B by species A then the appropriate temperature would be given when each species had correspondingly different innate capacities for increase. But in either case the situation would only hold provided the inhibition of one species by the other was directly proportional to the numbers of each species present, an assumption which has never been verified and which is almost certainly untrue. The proportional inhibition of one species by the other is much more likely to vary with density in a non-linear way, in which case the extent to which one species would be favored in comparison with the other would change as the population changed in size. The equilibrium, if it ever existed, would be upset immediately by any change in relative numbers of the two species.

Even if we assume that living animals possess the simple properties attributed to them by the theoretical model (in which the inhibition of one species is directly proportional to the numbers of the other species) it is extremely unlikely that the conditions of absolute constancy demanded by the model would ever be established in the laboratory. In other words the model is of theoretical interest only since it could never be verified empirically. It is not possible to maintain temperature, humidity, and quality of food constant in experiments with insects. These qualities fluctuate about a mean even in the best experiments. Under fluctuating conditions one species would have the advantage at one time and the other would have the advantage at the other time. A dynamic equilibrium between species might be established but it would be quite unstable since its continuance would depend upon the species surviving when the swing of the fluctuation happened to be against it. *D. melanogaster* and *D. funebris* may provide an example of this sort of association; Merrell (1951) found that these two species survived together when they were reared in population cages in which food was regularly renewed. The proportion of the two species fluctuated greatly between the limits 1.9 per cent to 94.2 per cent of *D. funebris.* Merrell suggested that the continued existence of the two species together might be due to the fluctuations of the quality of the food, for new food was known to favor *D. melanogaster* but the older food favored *D. funebris.* The regular renewal of food provided continuously changing conditions which favored first one species and then the other.

The experiments described in this paper may appear to provide results which could be used as a critical test of the Lotka-Volterra mathematical models. These are theoretical models which formulate a simple hypothesis of what happens when two species live together and seek the same

food. However, Andrewartha and Birch (1953) have shown that there is a fundamental contradiction in these models which renders them quite inadequate for the interpretation of laboratory experiments.

No mention has been made of the possibility of genetic changes in the composition of the populations of beetles in the experiments. This possibility is being investigated. Moore's (1952b) experiments demonstrated such changes in *Drosophila*.

Summary

When the beetles *Rhizopertha dominica* and the small and the large strains of *Calandra oryzae* lived together in the same experimental models feeding on the same grain, only one of the species eventually survived. This was the species which had the higher innate capacity for increase under the conditions of the experiment. Within the 15 replicates of any one series of experiments the same species always became extinct, the time for this to occur varied from a half a year to four years depending upon the conditions of the experiment. The end points of the experiments were reversed by altering the sort of food or the temperature so that the species which was successful when it had the higher innate capacity for increase became unsuccessful under conditions which gave it a lower innate capacity for increase as compared with the other species.

The large strain of *C. oryzae* was successful in the association—large and small strain, when they lived together in maize at 29.1° C. In maize it had the higher innate capacity for increase. But in wheat, under otherwise identical conditions, the small strain had the higher innate capacity for increase and it became the successful species. Similarly the small strain of *C. oryzae* is the successful species in wheat at 29.1° C. in the combination *R. dominica* and the small strain of *C. oryzae*. At 29.1° C. the small strain had the higher innate capacity for increase. But at 32.3° C. *R. dominica* had the higher innate capacity for increase and at this temperature it was the successful species.

The close correlation between innate capacity for increase and success in surviving may not be expected in other experimental models in which the successful species interferes with the other species in ways which cannot be predicted from their behavior when they live alone.

Acknowledgments

My thanks are due to Dr. H. G. Andrewartha of the Waite Institute, University of Adelaide, for his helpful criticism of the manuscript.

Literature Cited

Andrewartha, H. G. and L. C. Birch. 1953. The Lotka-Volterra equations for competition. Aust. J. Zool., I. (In press.)

Birch, L. C. 1953a. Experimental background to the study of distribution and abundance of insects. I. The influence of temperature, moisture and food on the innate capacity for increase of three species of grain beetles. Ecology. (In press.)

Birch, L. C. 1953b. Experimental background to the study of distribution and abundance of insects. II. The relation between innate capacity for increase and the abundance of three grain beetles in experimental populations. Ecology. (In press.)

Birch, L. C., T. Park, and M. B. Frank. 1951. The effect of intraspecies and interspecies competition on the fecundity of two species of flour beetles. Evolution, **5**: 116–132.

Dobzhansky, Th. 1950. Heredity, environment and evolution. Science, **111**: 161–166.

Merrell, D. J. 1951. Interspecific competition between *Drosophila funebris* and *Drosophila melanogaster*. Amer. Nat., **85**: 159–169.

Moore, J. A. 1952a. Competition between *Drosophila melanogaster* and *Drosophila simulans*. I. Population cage experiments. Evolution, **6**: 407–420.

Moore, J. A. 1952b. Competition between *Drosophila melanogaster* and *Drosophila simulans*. II. The improvement of competitive ability through selection. *Proc. Nat. Acad. Sci.*, 813–817.

Park, T. 1948. Experimental studies of interspecies competition. I. Competition between populations of the flour beetles *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. Ecol. Monogs., **18**: 265–308.

Thompson, W. R. 1939. Biological control and the theory of the interaction of populations. Parasitology, **31**: 299–388.

Ullyett, G. C. 1950. Competition for food and allied phenomena in sheep blowfly populations. Phil. Trans. Roy. Soc. Lond., B., **234**: 77–174.

ON THE ORIGIN AND COMPOSITION OF THE NEARCTIC INSECT FAUNA

HERBERT H. ROSS
Illinois Natural History Survey, Urbana, Illinois

Received January 15, 1953

INTRODUCTION

Students of paleoecology of the ocean have enjoyed two distinct advantages over those trying to synthesize similar information concerning terrestrial habitats. First, there live today a host of oceanic creatures whose fossil record extends virtually unchanged far into the past so that one can extrapolate with considerable certainty from demonstrated ecological tolerances of present-day organisms back to earlier ages. Secondly, the oceans have provided a more complete and continuous fossil record of their life, whereas during many periods the lands have been niggardly in preserving recognizable fossils.

In attempts to supplement our knowledge of past ecological conditions on the land, it will probably be found that different groups of organisms shed particular light on some specific aspect of the subject. It is further reasonable to predict that insects will ultimately be of the utmost assistance in providing information that will help us to roll back portions of the curtain of time. Not only do insects constitute by far the greatest part of the world fauna, but the various individual genera or species groups have rigid ecological tolerances of almost every combination imaginable.

The relatively great age of existing insect genera is only now being realized. It is probable that most of them are at least of Oligocene age, and many date back to the Cretaceous or even earlier. This gives some promise of information about that period between the latter part of the Age of Reptiles and the time when mammals first become well represented in the fossil record, a period poorly known now as regards terrestrial life.

Insect fossils form a highly discontinuous record. In many cases the fossils are fragmentary, showing few needed characters, so that studying them is oftentimes a frustrating experience. Other approaches are therefore necessary, and that of biogeography is proving most fruitful. True, it must be used with caution, and results obtained by it will need constant checking, correcting, and rechecking. But there is no doubt that it can contribute many novel and profitable ideas on the biotas of past eras and the dispersal patterns of living things that have spread from continent to continent.

It is my hope in this paper to point out particularly some of these dispersal patterns, to show some of the interesting problems that have arisen, and to stimulate more work in this fascinating and provocative field.

THE NEARCTIC INSECTS

The nearctic insect fauna is a large one. It includes roughly 30 orders and 500 families, comprising about 12,000 genera and 125–150,000 species. This last figure is about a sixth of the estimated total number of insect species already described in the world.

You might think that with such a huge fauna already known, we would have a correspondingly large store of information regarding the origin and dispersal patterns of insects, but in reality such knowledge is peculiarly spotty. The most extensive attempt to bring together such data was by E. C. Van Dyke in 1939, when he outlined his ideas of the origin of the Nearctic beetle fauna. He concluded that the Coleoptera comprised eight distinct faunas in the Nearctic region, five coming via the north and northwest from Eurasia, three coming from South America, and that of these, certain forms arrived as early as

Oligocene, but the greater part not until Pliocene or Pleistocene. Studies of this type are excellent for indicating the degree of relationship between faunas of different areas, but they fail to show in which area the original fauna developed. It is interesting that Van Dyke thought that all our forms had entered North America from other areas, almost as if it had contained no modern forms prior to 30 or 40 million years ago.

In the same year H. B. Mills made an interesting study of the Nearctic springtails. He concluded that the greatest affinities of the Collembola were with the European fauna, not the Asiatic, and drew attention to the interesting fact that the northern fauna contained a high proportion of primitive forms and the southern fauna a high proportion of specialized forms, completely at variance with the Matthewsian contentions regarding distribution. Both of these valuable papers suggest a host of intriguing questions. I believe this phrase "a host of intriguing questions" sums up the situation regarding our knowledge of the origin of the Nearctic fauna.

The Fossil Record

The North American fossil insect record gives some hints of great interest. At Mazon Creek, Illinois, there occur fossils of Pennsylvanian age. At Elmo, Kansas, was found one of the richest deposits of insect fossils of Permian age. Both of these are in the Paleozoic era. The fauna represented by these deposits belongs to archaic families or orders since extinct, with the exception of the cockroaches which are remarkably similar in general appearance to those found today. Based on tunnels preserved in petrified wood, we know that bark beetles and flatheaded borers occurred in Arizona in the Triassic. Without knowledge of the adult structure, it is impossible to relate these early American beetles with any existing subfamilies or genera, but it is certain that the modern families Scolytidae (bark beetles) and Buprestidae (flatheaded borers) were differentiated at that time and present in North America. There are a few Cretaceous fossils from Tennessee and Canada, in both cases the majority of forms representing existing subfamilies or genera. Cenozoic insect fossils are found in many areas, and are especially well known from Florissant, Colorado. These represent chiefly genera found today. This is well substantiated in groups such as the termites in which generic and specific characters can be seen in the fossils (Emerson 1933). The large number of strange generic names found applied in many groups is due primarily to our inability to be sure of the exact placement of the fossils because in these groups the fossils do not show critical diagnostic characters.

In this record there is not a sufficient sequence of forms to be able to follow changes in the composition and structure of any single group. The record does show one fact of importance, namely, that North America has had a continuous insect fauna since at least late Paleozoic, and a fauna embracing modern families since early Mesozoic. In other words, the continent has not been an entomological vacuum which had to be filled from outside sources; it is entirely conceivable that much of our fauna originated here.

The Living Record

In the present incomplete state of our knowledge of insect distribution, I believe the most practical method of demonstrating the origin of part of the Nearctic fauna is to examine a few groups for which sufficient information is available. These are cases in which geographic distribution of a group for the entire world has been charted in comparison with phylogeny to determine the dispersal pattern. These patterns have then been correlated with either dated dispersal patterns of other organisms (plant or animal) based on fossil records, or with evidence of a geological nature concerning the connection or separation in past times of neighboring

land areas. In some cases a reasonable hypothesis may be deduced for the movement in time of the group under scrutiny.

The success of applying this method is due to the unusual survival pattern found in insects. In many groups, species or genera have survived to such an extent as to give us a living portrayal of the actual path of evolutionary change. In other words, there are living today forms little different from the hypothetical ancestors of the group which lived as long as 80 or 100 million years ago, as well as younger forms and species representing all intermediate stages. This phenomenon of living chainlike aggregates of annectant forms has been recognized for some time (Kinsey, 1936; Ross, 1929, 1937), but for many reasons it has been used for interpretation in only a limited number of cases.

The individual case histories that follow are based on the most up-to-date information that I have been able to assemble on each group. The results are nevertheless preliminary, because there are many areas of the world that have been little collected, and in practically no area have collecting possibilities been exhausted. There are equally serious limitations on the number of characters available for analysis in various groups. It is entirely possible with insects, as with any other group, to work out a phylogenetic scheme that seems perfect on the basis of the characters employed, but which scheme proves to need serious reshaping when other characters become known. A biogeographic analysis is no better than the phylogeny on which it is based. Both of these limitations are products chiefly of the overwhelming diversity of the insect group. In a way this is unfortunate, but on the other hand we are indeed blessed to have this store of potential information available.

The Agapetini

A fairly simple dispersal pattern is exemplified by a group of caddisflies, the tribe Agapetini belonging to the family

FIG. 1. Dispersal pattern of the Agapetini (from Ross 1951*b*)

Rhyacophilidae. The Agapetini are small forms whose larvae make saddle-like cases and frequent cold, clear streams in both montane and hilly country.

There are two genera of Agapetini in the Nearctic region, the genus *Anagapetus* occurring in the western montane region, and the widespread genus *Agapetus* which occurs in both eastern and western North America. In Eurasia there are two other genera, *Catagapetus* and *Electragapetus,* many species of *Agapetus,* but no known forms of *Anagapetus.* When we outline the phylogeny of the group it is evident that *Anagapetus* is extremely similar to the original ancestor of the entire tribe; that *Catagapetus* and *Electragapetus* represent stepping stones in the direct line of development from *Anagapetus* to *Agapetus;* and that the American forms of *Agapetus* do not represent early and primitive branches of the genus but instead arose from a later and highly specialized group. It should be noted that there is a Baltic amber species, *Electragapetus scitulus*

Ulmer, which provides a definite fact of great assistance in attempting to date the sequence of events. This is tabulated in Ross 1951*b*.

Reconstructing the dispersal of the group, figure 1, it seems highly probable that *Anagapetus* originated in North America very early in the Cenozoic if not in the Mesozoic, and spread into Eurasia at least by early Eocene. The Eurasian branch evolved at a fairly rapid rate, giving rise to *Catagapetus,* then *Electragapetus,* and finally to *Agapetus.* The genus *Agapetus* continued to evolve, giving rise to several lines, one of which spread back into North America probably in Oligocene or early Miocene, and was the parent of our present fauna of about 20 species. Thus we have a Nearctic fauna of dual origin, the first part probably starting here, the second representing a mid-Cenozoic dispersal from Eurasia.

The genus ERYTHRONEURA

The leafhopper genus *Erythroneura* contains about 500 species, most of which feed on deciduous trees, shrubs, or vines. It constitutes one of the most abundant leafhopper genera in eastern North America. Within the broad framework of the genus, about twenty species groups are recognized, some containing only one or two species, others containing as many as 150. Certain groups are quite restricted in distribution and aid in deducing the origin of the fauna of different areas. In Europe the genus is represented by some 40 or 50 species, distributed in about a

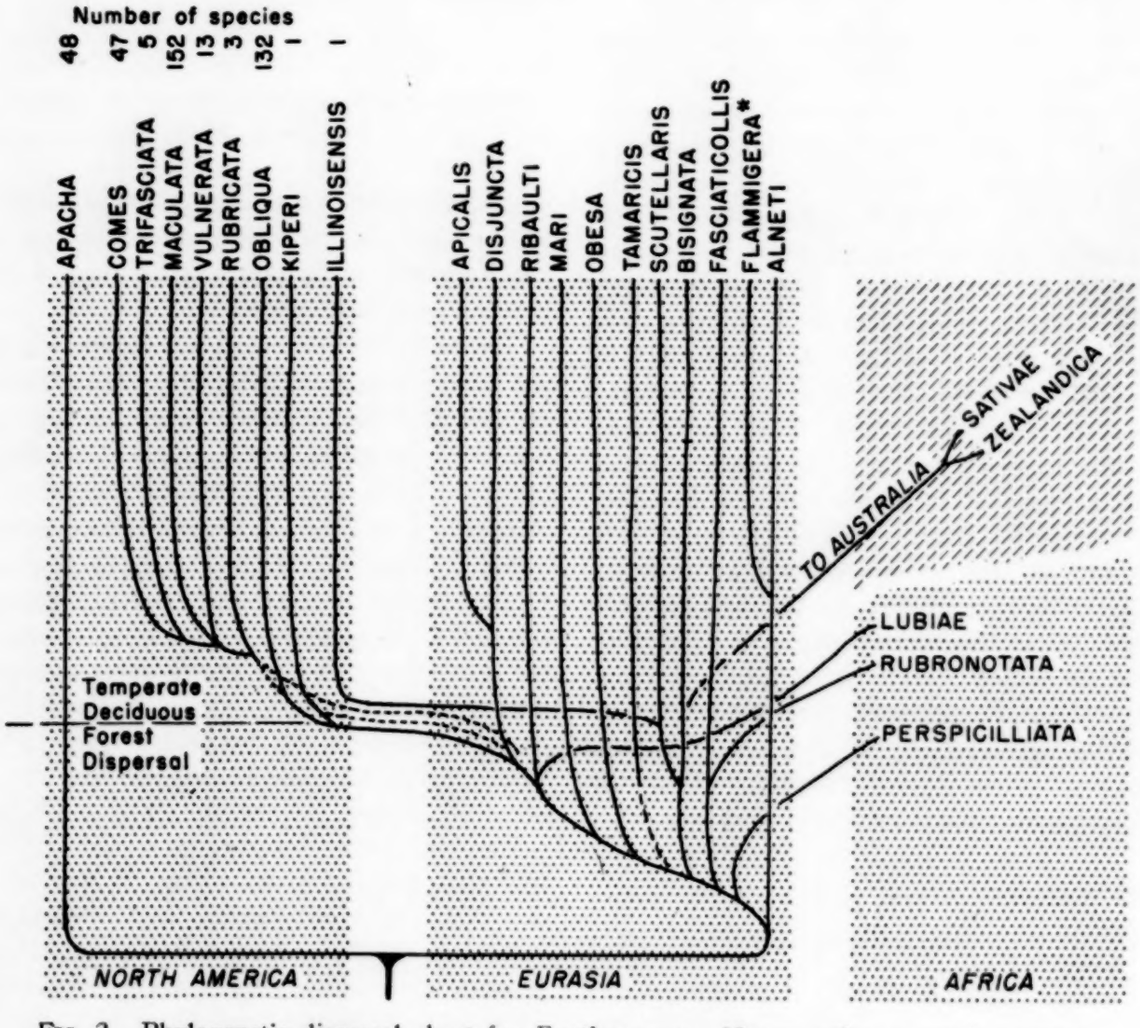


FIG. 2. Phylogenetic dispersal chart for *Erythroneura.* Names refer to species groups.
* Introduced by man into North America.

dozen small groups. The meager known fauna of Africa and Asia contains a scattering of these same groups, and the few species in the Australian region are from two or three of these also. In the southwestern portion of North America there are about 50 species of a very primitive group, which also contains one known species from Honduras and another from Argentina. In the eastern portion of North America the genus really blossoms. Here there is an assemblage of over 350 species, belonging with only one exception to seven highly specialized and closely related groups known from no other part of the world.

As with many other insects, the structures of the male genitalia of this genus offer excellent characters for tracing its evolutionary development, and there are existing today species which illustrate almost every intergradation from the most primitive to the most specialized condition. When the phylogenetic relationships so deduced are plotted against geographic distribution, a most intriguing dispersal pattern is suggested, figure 2.

The exact origin of the genus is uncertain, but it seems clear that in early Cenozoic or even earlier a primitive form of the genus spread between Eurasia and North America and was soon isolated, one population in each continent. The North American segregate developed into the *apacha* group. This group, still very primitive in structure, is at present found in the Southwest. The Eurasian segregate began a series of evolutionary changes which finally produced the *disjuncta* group. One or more species of this group evidently spread to North America, where they evolved into several more specialized groups. Of these the *obliqua* group is very similar to its *disjuncta* progenitor, but the *comes* and *maculata* groups are much different in structure of genitalia. Altogether, the North American groups have now evolved into over 350 species, almost entirely in the eastern deciduous forest. In spite of their abundance in America, none of these Nearctic species have spread back into the Palearctic region, on the basis of known records.

From this it seems highly likely that the colonizers from the *disjuncta* group spread to the Nearctic region at the time when the temperate deciduous forests formed a continuous band across both North America and Eurasia. Paleobotanists consider this to be in either Eocene or Oligocene times. It is likely that the progenitor of *illinoisensis,* a close relative of the Eurasian *scutellaris* group, spread into North America at the same time, even though this branch is now represented in North America by only one species.

Species flocks. The three large and more recent groups of *Erythroneura* introduce an intriguing concept concerning the evolution of terrestrial animals. The *obliqua, comes,* and *maculata* groups apparently originated about Miocene in the eastern deciduous forest and have been rigidly confined to it ever since. During this period the *obliqua* group has evolved into about 140 species, the *comes* group into about 50, and the *maculata* group into about 150 species. Only a few highly specialized forms have spread into other areas. This phenomenon is homologous both in structure and implications to the famous species flocks of aquatic animals developed in Lakes Baikal, Nyasa, Tanganyika, and others (Brooks, 1950). This idea of species flocks certainly is applicable to many groups of insects, and probably applies also to such aggregations of vertebrates as the salamanders of the southeastern United States.

The gall wasp genus CYNIPS

It is axiomatic that bridges have two ends and therefore two approaches. For this reason we would expect that organisms on either side of a land bridge would disperse across it. A dispersal complementary to the eastward spread of specialized *Erythroneura* into North America about Oligocene times is found in the gall wasp genus *Cynips,* which appears to have spread from North America into Eurasia at the same time.

In his studies on this genus, Kinsey (1930, 1936) considers that the genus *Cynips* originated in Mexico, and early divided into two lines. One of these eventually spread to Eurasia, possibly in Oligocene; the American populations of this line developed into the western subgenera *Antron* and *Besbicus,* the Eurasian into the subgenus *Cynips*. The other line apparently did not spread beyond North America. On this continent it developed into three groups, the subgenera *Atrusca, Philonyx,* and *Acraspis*. The primitive members of all three groups occur in Mexico, with more specialized forms occurring northward and extending into the southeastern states. Due to the speciation pattern in this latter area, Kinsey considered that the dispersal of *Cynips* into the Southeast occurred before the Pleistocene. From these data it seems certain that all the early development in the genus took place in the Southwest and/or Mexico, and that populations of individual species

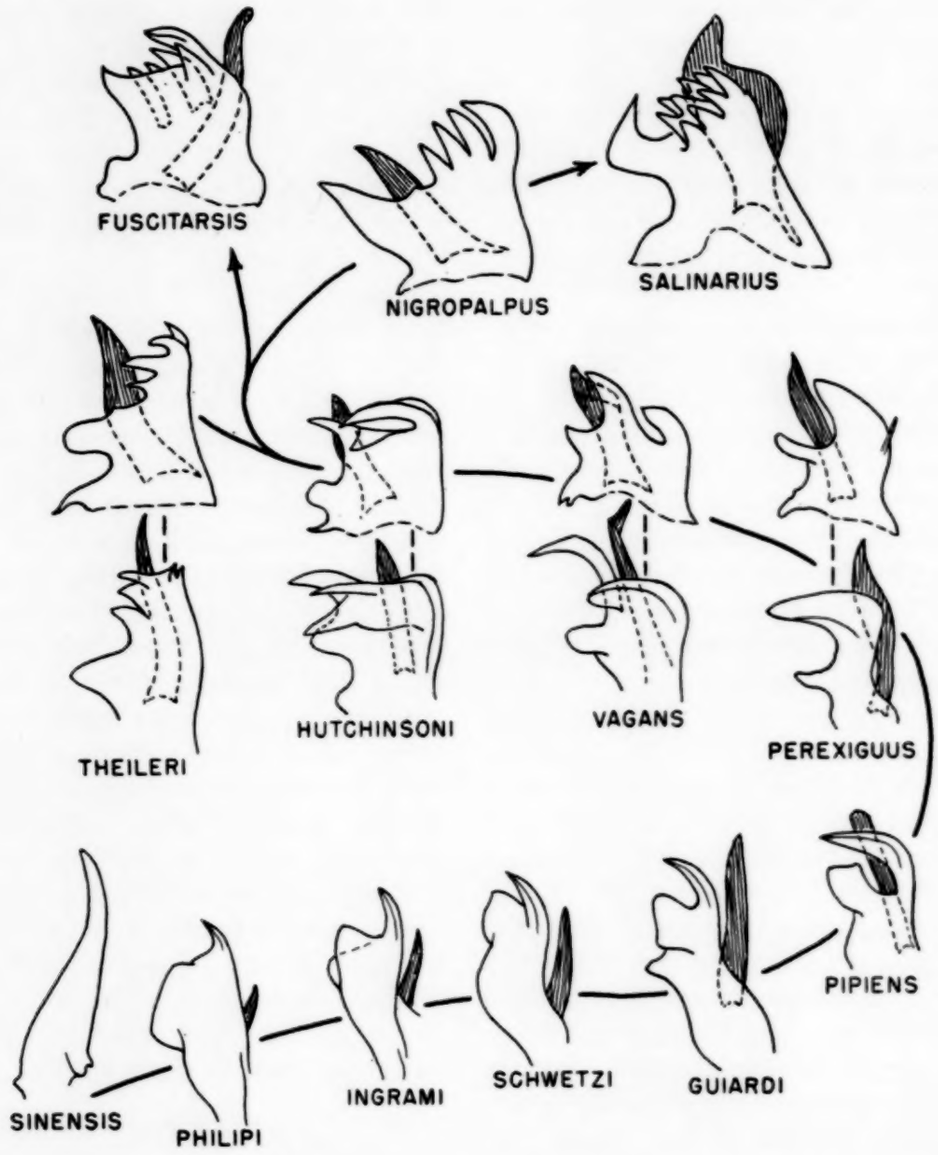


FIG. 3. Male genitalia of key species in *Culex pipiens* line. Upper two rows, lateral aspect; lower two rows, ventral aspect. Parts redrawn from Barraud 1934, Edwards 1941, Carpenter *et al.* 1946, and Ross 1947.

spread into other areas, became isolated there, and evolved into more specialized types.

The genus CULEX

The Nearctic mosquitoes consist of only about a dozen genera, but most of these genera are almost world-wide in distribution. This would indicate either great antiquity of origin or unusually effective dispersal of mosquito species. If we study the problem further, we find that a few genera are of limited distribution and within the large genera some species groups are likewise restricted. An analysis of these groups leads to the preliminary conclusion that the Nearctic fauna may be divided into some well-marked general categories, as follows:

1. Certain widespread cool-adapted forms, such as *Aedes vexans* and the genus *Culiseta,* form part of a northern, Holarctic faunal unit, part of which probably originated in North America.

2. Some tropical groups, such as *Psorophora* and *Culex* subgenus *Melanoconion* evidently arose in Central or South America, and have spread northward from those areas.

3. Genera such as *Mansonia* evidently arose in the Oriental region or Africa, and subsequently spread to North America.

4. A few complexes of Arctic species of *Aedes* and *Culiseta* may have arisen in the far northern portion of North America during the interglacial epochs.

This sounds very straightforward and simple, but if we examine the origin and composition of the Nearctic species of an individual genus, they frequently are found to be the result of a complicated evolutionary pattern. A good example is the *Culex pipiens* line. The genus *Culex* evidently divided early into several main branches. One became established in tropical America, developing into *Melanoconion* and its allies. A second line apparently became established in the Old World, developing into *Neoculex* and its allies, and *Lutzia.* A third branch, also in the Old World, developed into the typical subgenus *Culex.*

Primitive forms of this subgenus, exemplified by the Oriental *sinensis* and Nearctic *restuans,* apparently spread to

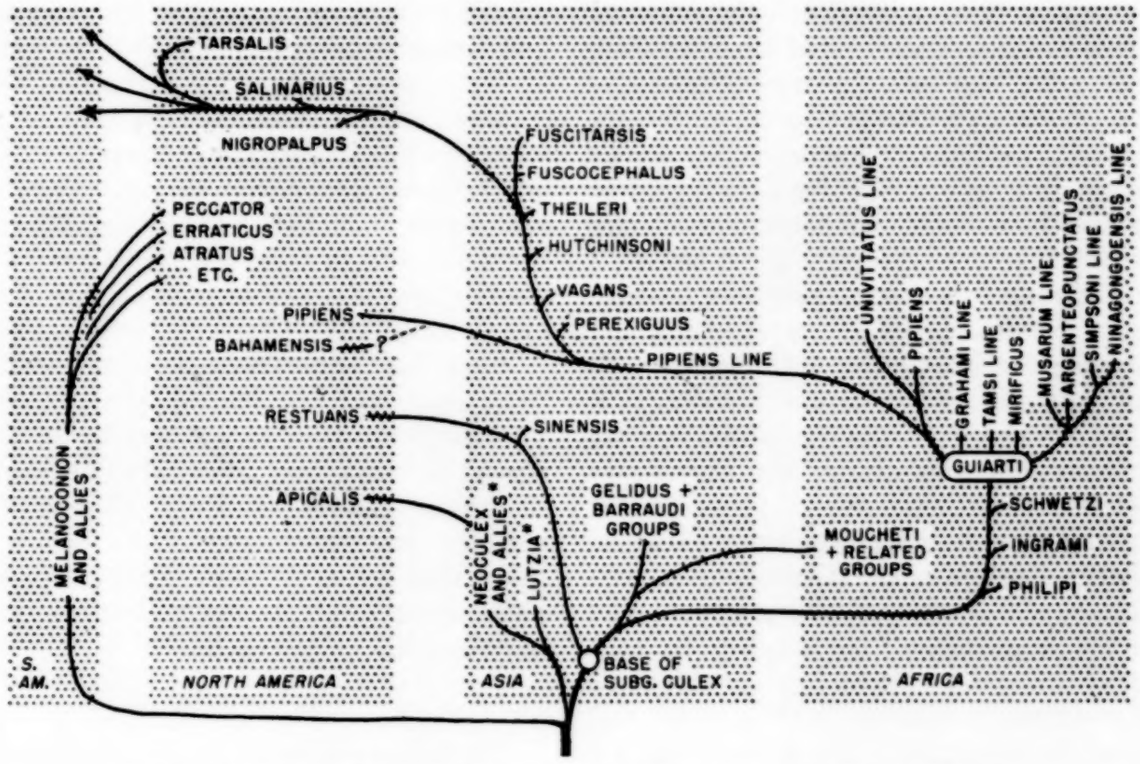


FIG. 4. Phylogenetic dispersal chart for *Culex.* * Occur also in Africa.

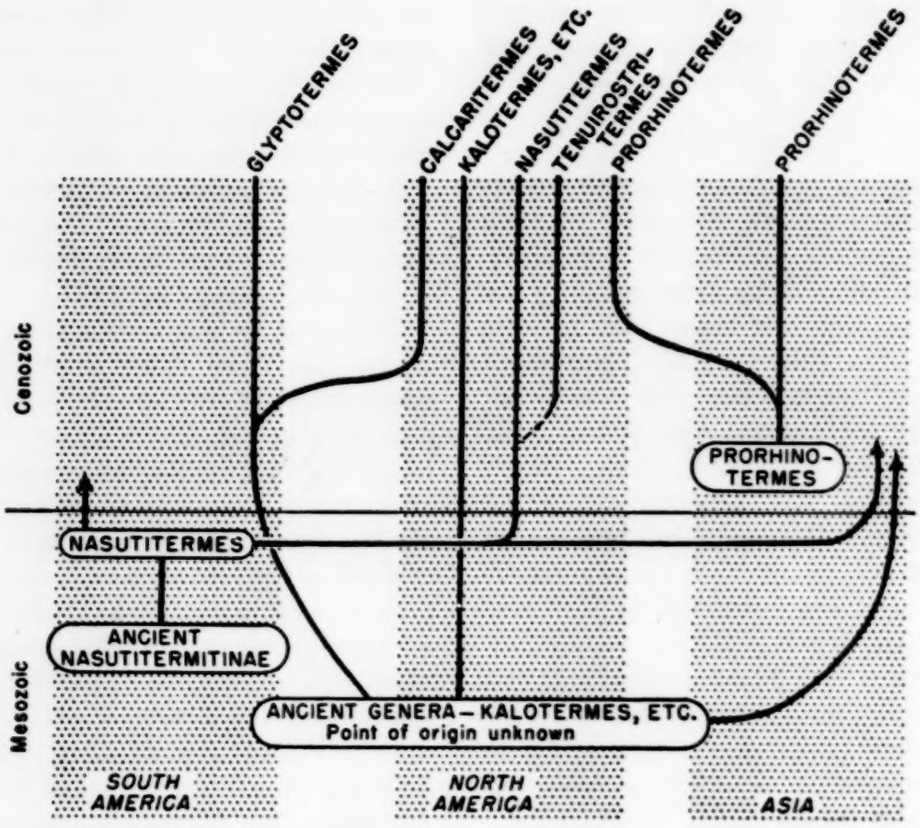


FIG. 5. Phylogenetic dispersal chart for certain Nearctic termites and their parent genera.

various areas and started new evolutionary lines. So perfect has been the survival of much of this branch, that we can follow the ensuing evolutionary pattern by studying progressive changes in structures of the male genitalia, a few of which are illustrated in figure 3. The particular line in which we are interested apparently spread to Africa, where it gave rise to a line leading to a species very like *guiardi*, figure 4. From this ancestral form there developed at least seven different lines, all but one remaining confined to Africa. The exception was the line producing the ancestor of *pipiens*, which apparently spread to India and there started a new evolutionary line leading from ancestral *pipiens* through ancestral *perexiguus* to a form similar to *theileri*. This form spread to the Americas, where it gave rise to a series of species including the Nearctic *nigropalpus*, *salinarius* and *tarsalis*, and other Neotropical forms. Were it not for the survival of connecting links in Africa and Asia, we might think that this *salinarius* group originated in South America and spread into North America, whereas actually the opposite seems to be the case.

Summarizing the data for *Culex* alone, we find that the Nearctic fauna is composed of elements from various lines of the genus, including (1) several species of *Melanoconion* from the Neotropical region, (2) one species of *Neoculex* (*apicalis*) from Asia, (3) a primitive species of subgenus *Culex* (*restuans*) presumably from Asia, and (4) several species of the *pipiens* line which originated in Africa, spread to Asia, and from there to North America. I have made no effort to try to date this pattern except to hazard a guess that it covers most of the Cenozoic, and that the original dispersal of the genus may have been even earlier.

The termites

The termite fauna of the Nearctic region contains about 15 genera, in an eco-

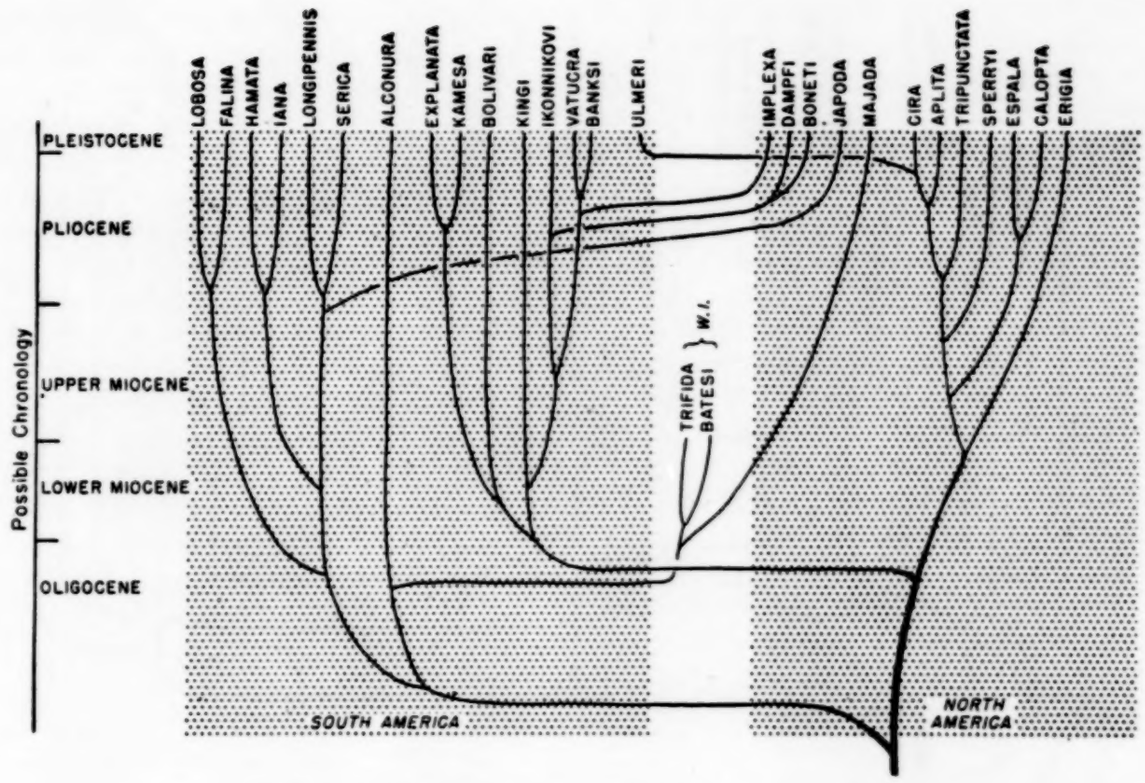


FIG. 6. Phylogenetic dispersal chart for *Atopsyche*.

logical sense forming a fairly compact subtropical unit with a few extensions into the warm temperate zone. In a recent study, A. E. Emerson (1952) has outlined his great pioneering ideas concerning the origin and dispersal of most of these genera, and these ideas are summarized here. Dr. Emerson believes that the termites are an old group, existing families dating back to at least early Mesozoic, which is far earlier than any known fossil records. The genera in the Nearctic region arose at various times, figure 5, and from four of the five known termite families. Genera such as *Kalotermes, Cryptotermes,* and *Neotermes* are nearly world-wide; they probably arose in middle Mesozoic and dispersed to various areas of the world in the Jurassic or Cretaceous over the Bering bridge. The point of origin of these groups cannot be determined because the most primitive genera of their family are widespread. The genus *Calcaritermes* is an offshoot of the tropicopolitan genus *Glyptotermes*. *Calcaritermes* probably arose in Central America during the Tertiary and has spread into the Nearctic region from there. The genus *Prorhinotermes* is a peculiar genus apparently distributed in floating logs. It is primarily confined to islands but is present on the coast of Central America and Florida. Dr. Emerson believes that the genus arose in the Pacific Islands, spread along the coast line and probably reached the Caribbean area through one of the ocean connections through the Panama region during Tertiary times.

Another type of dispersal is exemplified by the nasute termites of the subfamily Nasutitermitinae. The primitive members arose in South America and from these there eventually evolved genera such as *Nasutitermes,* which became world-wide. Later, in the Tertiary, other genera arose from these stocks, including the Central American genus *Tenuirostritermes,* which has spread into the Nearctic region.

The caddisfly genus ATOPSYCHE

There is more than usual importance attached to Emerson's suggestion that the

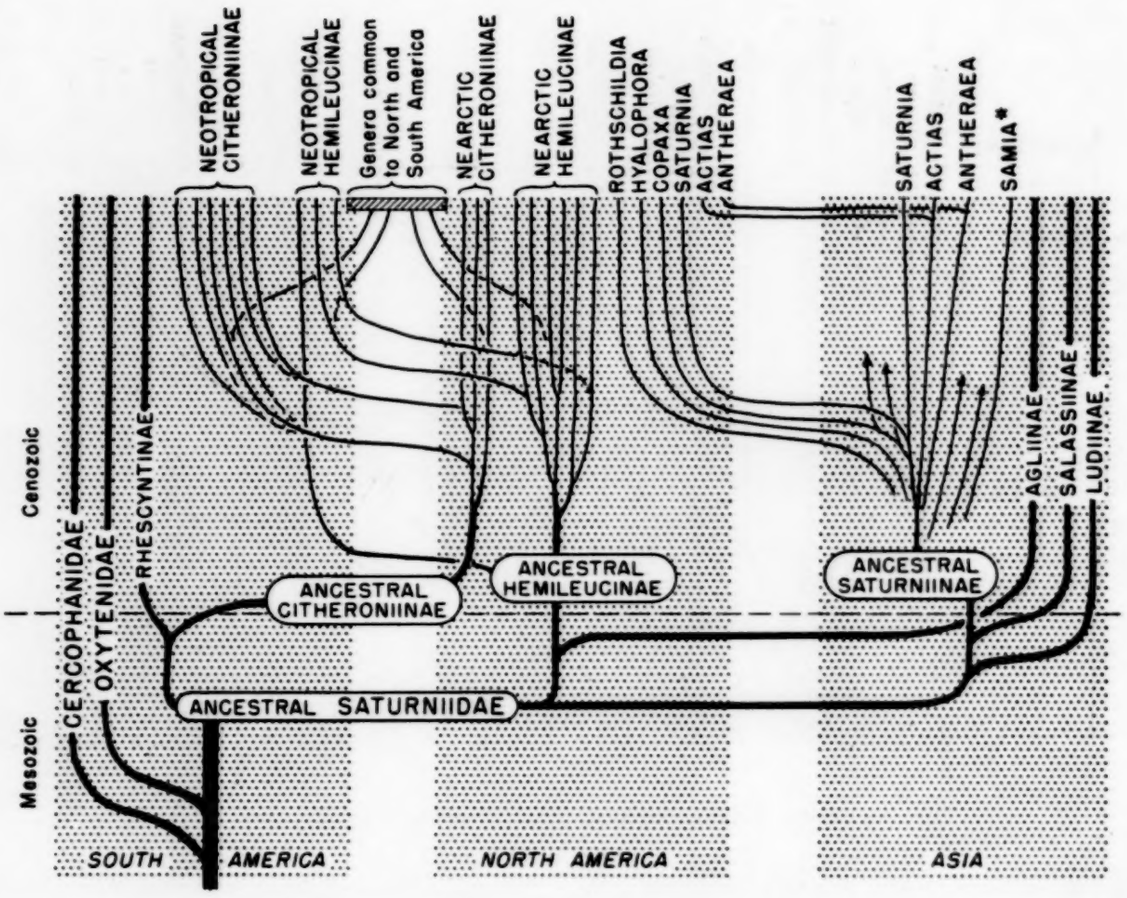


FIG. 7. Phylogenetic dispersal chart for the moth family Saturniidae.
* Introduced by man into North America.

more northern of the Neotropical groups had their origin in Central America, and I would like to explore this idea further with a group of caddisflies, the tribe Hydrobiosini. They are found only in clear, cool streams in the tropics or subtropics. The tribe has about nine Nearctic species, all belonging to the genus *Atopsyche* and occurring in the extreme southwestern portion of the continent.

The tribe appears to have originated in Asia. In late Mesozoic a primitive form apparently spread into Australia and North and South America (Ross, 1951a) giving rise in the Western Hemisphere to two South American genera, *Cailloma* and *Iguazu,* and a Central American genus *Atopsyche.* This latter genus is represented today by nearly 30 species with a total distribution from Arizona to Argentina and Peru. The phylogenetic tree suggests certain intercontinental movements, and these can be explained on a very reasonable basis by current concepts of land bridges between North and South America. The sequence of dispersal patterns is suggested in figure 6, modified from Ross & King, 1952, in which it is postulated that population interchanges between the Americas occurred in late Oligocene, lower Miocene, and again in Pliocene or Pleistocene. On this basis we have in the Nearctic region all the primitive members of the genus plus at least one species from each of the groups which developed specialized characteristics after spreading to and being isolated in South America. This seems a good example of the complexity which may arise in a group living in the Central American region.

The saturniid moths

An even more complex dispersal pattern is found in moths of the widespread family

Saturniidae. Using the phylogenetic tree and data on the range of each genus given in C. D. Michener's recent revision of the New World genera (1952), it is possible to construct a suggested dispersal pattern which combines several features we have just discussed, figure 7. The saturniid line apparently developed in South America, giving rise to the Cercophanidae, Oxytenidae, and then to the ancestral form of the Saturniidae. This ancestor must have had different ecological tolerances from the first two families, for it spread into North America and apparently into Eurasia. The intercontinental connections must have been broken soon after this, because the segregate on each continent developed into a separate line.

The South American segregate divided again into two groups. One became the subfamily Rhescyntinae which has remained restricted to South America. The other seems to have reached Central or North America and developed into the subfamily Citheroniinae, which has speciated into a large fauna. The North American population of the ancestral saturniid also seems to have given rise very early to a form which spread into Asia, the Asian segregate developing into the Agliinae, and the population remaining in North America becoming the large subfamily Hemileucinae. It is highly probable that dispersal up to this point was in the Mesozoic era, paralleling some of the termite distribution patterns.

The two subfamilies Hemileucinae and Citheroniinae seem to have behaved much like the *Atopsyche* caddisflies, spreading back and forth between North and South America as ecological conditions and land approximations permitted. This has resulted in an interwoven, complex dispersal pattern which for ultimate resolution will require a detailed study of species relationships. In both cases, however, the primitive forms are still primarily to the North and the highly developed genera are primarily in South America.

The phylogeny of the Old World fauna has not been worked out, but as Michener has said, it is clear that various lines of the Saturniinae spread back into North America. There was undoubtedly such a dispersal at the time of the Holarctic deciduous forest belt, before Miocene. At this time the progenitors of such Nearctic genera as *Rothschildia* and *Hyalophora* probably reached North America. Genera such as *Actias* and *Antheraea* have closely related species in both the Nearctic and Palearctic regions, and suggest a dispersal of forms in Pliocene or in one of the interglacial periods of the Pleistocene.

The Nearctic Saturniidae, then, had a multiple origin, stemming from two Central or North American branches and one Old World branch of the family. It is interesting to note that in many parts of the continent members of several groups occur in the same area, indicating that present Nearctic distribution alone is no criterion of the past history of a group.

Young Holarctic complexes

A large number of cool temperate and especially arctic species of insects are either Holarctic or belong to a tight complex of species which together have a Holarctic distribution pattern. In most of these cases it seems impossible to determine in which northern continent the species or complex originated.

Certain such species occur in pairs, one species occurring in Eurasia and Alaska, the other in the rest of northern North America, including Greenland. An example is the caddisfly pair *Limnephilus miser* from Eurasia and Alaska, and *Limnephilus kennicotti* from the Mackenzie Basin to Greenland. This suggests that prior to glaciation this pair was a single species which divided during the Pleistocene.

There is little doubt that some Eurasian species have spread into North America during very recent times. The great bulk of the species thought to be in this category occur predominantly in the Northwest, and so it is assumed that they spread into this continent from Asia via Alaska. There is, however, at least a small trickle

from the other direction. In a recent study of the west Greenland fauna, Vibe (in litt.) found all the species to be North American with the exception of one, *Limnephilus griseus,* common on Iceland and widespread in Europe. It is difficult to explain this discovery except as the result of a recent immigration from Europe via Iceland.

Ancient Holarctic complexes

Up to this point we have made no mention of one of the most distinctive features of insect distribution, and that is the occurrence of extremely ancient forms in northern and montane areas. An example is the caddisfly *Paleagapetus,* a veritable living fossil, known only from fossils from Baltic amber and living Nearctic species in the Cascade Mountains and the Allegheny Mountains. This genus is one of the most primitive known forms of the archaic family Rhyacophilidae. Another caddisfly example is the widespread eastern Nearctic genus *Phylocentropus,* known otherwise only from Baltic amber and very probably an Upper Cretaceous fossil from Tennessee. This genus is an exceedingly primitive member of the Psychomyiidae. It is of note that in both of these cases one of the Nearctic species is practically conspecific with a Baltic amber species. Numerous additional cases occur in the caddisflies and a goodly number in the sawflies. The figures given by Mills (1939) for primitive northern springtails undoubtedly include a large number of examples of this category.

It seems highly likely that these groups have been persistent members of the Nearctic fauna since middle or early Mesozoic.

In the case of the caddisflies and sawflies, many of these primitive, cool-adapted forms gave rise to offshoots which evolved into warm adapted groups that have become abundant in the faunas of subtropical and tropical areas. This is probably a common evolutionary pattern in other orders, such as the Diptera, in which some of the primitive groups are cool adapted.

Species introduced by man

In this account we should not forget the species which are transported by man from one part of the globe to another. It is perhaps conservative to estimate that well over a thousand species have been introduced into the Nearctic region in this fashion. Certain of them appear to be rigidly confined to introduced crops which can be maintained only under cultivation. Such insect species may never become part of the wild fauna. The great majority of introductions, however, can exist on some native hosts, or are sufficiently general feeders that specific food is no problem. These will become a part of the permanent fauna just as readily as if they had walked or flown over a land bridge. It is of special interest to note that many of these introductions represent phyletic lines not previously known from the Nearctic region (note figs. 2 and 7).

Composition of the Nearctic Fauna

Although the title of this paper is "Origin and Composition of the Nearctic Insect Fauna," up to this point we have mentioned nothing about composition. Let us now examine this possibility. In the preceding cases we have mentioned casually a few thousand species, but have attempted some detail of analysis for only six groups, and mentioned specific examples of a few other species. The total in species is only 774. Since the total insect fauna of the area is about 150,000 species, we have dealt with only 774/150,000 of the fauna, or .51%. This leaves unaccounted for 99.49% of the fauna. It seems to me a little presumptuous to make any statements about percentage composition of the fauna on the basis of such a small sample. This is especially true when we realize that the small available figure has a marked bias towards subtropical groups, with extremely little detailed information available for cool-adapted groups.

There are a few other groups not mentioned in this paper for which some information is available, but I doubt if they

would change our percentage to any great degree.

General Comments

Comparing these insect dispersal patterns with each other and with data from other groups, a few comments seem in order on several points.

Age of insect fauna. Much of the insect fauna is so old that we have no basis for even guessing at its place of origin or early dispersal pattern. This includes not only tropical insects such as primitive termites, but also many cool-adapted forms which presumably date back to middle or early Mesozoic. This is reminiscent of the eulamellibranch Mollusca.

Complexity of fauna. For a limited number of insect groups, dispersal patterns can be plotted with considerable assurance back to early Cenozoic or late Mesozoic. These examples indicate that there is a high degree of individuality as to the origin of the Nearctic fauna of each group, and that the Nearctic fauna had a complex origin, including endemic groups and colonizations at many times from Asia, Europe, and South America. The complexity of this pattern in insects suggests that the system of a few "time faunas" as used in studies of birds and reptiles (Smith, 1949; Griscom, 1950) is an oversimplification in regard to categorizing the entire biota of the whole Nearctic area.

Effects of glaciation. There occur aggregations of closely related species forming true species flocks that have been restricted to the eastern deciduous forest since approximately the Miocene. The persistence of such numerous and complex flocks indicates that the glacial ages of the Pleistocene caused neither wholesale extermination nor wholesale migration out of the temperate region on the part of the insect fauna. The chief effects of the glaciers on these organisms would seem to be

(1) the multiplication of some species, due to various processes of speciation.

(2) the reduction of the area of each eastern community, but the elimination of none. Contrary to what seems to be general opinion, there is every reason to believe that this reduction of range proceeded in an orderly fashion following normal population dynamics, and not as the melodramatic seething struggle of mingled faunas pictured by many writers.

(3) the spread of some groups southwestward into the Ozarkian uplift and Texas crosstimbers, but probably little or no farther. At all events, it seems certain that at most four or five species of *Erythroneura* spread into more westerly deciduous forest areas. In the eastern species flock *Pycnopsyche* in the caddisflies there is no evidence of spread even as far west as Texas.

These conditions seem to be the only postulates that will explain the survival pattern in *Erythroneura, Agapetus,* and several other groups not treated in this paper. These same groups also substantiate to a remarkable degree the concept of southeastern United States as an important area for the genesis and dispersal of groups as advanced by Adams (1902).

Future possibilities. Even at the expense of belaboring the point, I must emphasize the fact that we have made only a small beginning in understanding the dispersal dynamics of the insects. The amount of good information waiting to be discovered staggers the imagination. This will not be easy work, but the results will unquestionably contribute significantly to a better understanding of the evolution and dispersal of living things.

Acknowledgments

I wish to express my thanks to Dr. P. F. Mattingly for sending me information on mosquito types in the British Museum, to Dr. A. E. Emerson and Dr. H. B. Mills for opportunities to talk over different points in the manuscript, and, for this same aid, members of our local insect evolution discussion group.

Literature Cited

Adams, C. C. 1902. Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull., **3**: 115–129.

Barraud, Capt. P. J. 1934. The fauna of British India, including Ceylon and Burma. Diptera. V. Family Culicidae. London, Taylor and Francis. 463 pp.

Brooks, J. L. 1950. Speciation in ancient lakes. Quart. Review Biol., **25**: 30–60, 131–176.

Carpenter, Stanley J., Woodrow W. Middlekauff, and Roy W. Chamberlain. 1946. The mosquitoes of the southern United States east of Oklahoma and Texas. Amer. Mid. Nat., Monograph no. 3. 292 pp.

Edwards, F. W. 1941. Mosquitoes of the Ethiopian region. III. Culicine adults and pupae. London: British Museum (Natural History). 449 pp., 3 pls.

Emerson, Alfred E. 1933. A revision of the genera of fossil and recent Termopsinae. Univ. Calif. Publ. Ent., **6** (6): 165–196.

——. 1952. The biogeography of termites. Bull. Amer. Mus. Nat. Hist., **99**: 217–225.

Griscom, Ludlow. 1950. Distribution and origin of the birds of Mexico. Bull. Mus. Comp. Zool., **103**: 341–82.

Kinsey, Alfred C. 1930. The gall wasp genus *Cynips*, A study in the origin of species. Ind. Univ. Studies, **16** (Studies Nos. 84, 85, 86). 577 pp.

——. 1936. The origin of higher categories in *Cynips*. Ind. Univ. Publ., Science Ser., **4**: 1–334.

Michener, Charles D. 1952. The Saturniidae (Lepidoptera) of the western hemisphere, morphology, phylogeny, and classification. Bull. Amer. Mus. Nat. Hist., **98**: 339–501.

Mills, Harlow B. 1939. Remarks on the geographical distribution of North American Collembola. Bull. Brooklyn Ent. Soc., **34**: 158–161.

Ross, Herbert H. 1929. Sawflies of the subfamily Dolerinae of America north of Mexico. Ill. Biol. Monographs, **12** (3): 1–116.

——. 1937. A generic classification of the Nearctic Sawflies (Hymenoptera, Symphyta). Ill. Biol. Monographs, **15** (2): 1–173.

——. 1947. The mosquitoes of Illinois (Ditera, Culicidae). Bull. Ill. Nat. Hist. Surv., **24**: 1–96.

——. 1951a. The origin and dispersal of a group of primitive caddisflies. Evolution, **5**: 102–115.

——. 1951b. Phylogeny and biogeography of the caddisflies of the genera *Agapetus* and *Electragapetus* (Trichoptera: Rhyacophilidae). Jour. Wash. Acad. Sci., **41**: 347–356.

Ross, Herbert H., and Edwin W. King. 1952. Biogeographic and taxonomic studies in *Atopsyche* (Trichoptera, Rhyacophilidae). Ann. Ent. Soc. Amer., **45**: 177–204.

Smith, Hobart M. 1949. Herpetogeny in Mexico and Guatemala. Ann. Assoc. Amer. Geog., **39**: 219–238.

Van Dyke, Edwin C. 1939. The origin and distribution of the coleopterous insect fauna of North America. Proc. Sixth Pac. Sci. Con., **4**: 255–268.

THE EVOLUTION OF THE MAMMALIAN EAR

D. M. S. Watson

Department of Zoology, University College, London

Received September 22, 1952

Introduction

Recent discussions of the mechanisms which have brought evolution about have led to a wide spread concurrence of opinion about the factors involved in the production of geographical races and the isolation of species, but they have not achieved the same general acceptance in their consideration of major evolutionary events, the coming into being of the various phyla or of such a class as the Mammalia, or of such great steps as the evolution of the craniate eye. Here a different process, with a different mechanism "macro-evolution" has been invoked by some workers.

It is evident that we shall never know the steps which led up to the craniate eye, but we can expect to see and to understand much of the evolutionary history of the sound transmitting mechanism of the mammalian middle ear, one of the great steps for which an independent macro-evolution is invoked.

The problems presented by the evolution of the mammalian middle ear may be stated historically as follows: In 1601 A.D., J. Casserius showed that mammals possessed three bones in their middle ear, and birds, as represented by a goose, only one. By 1800, names had been given to these elements, and it had been recognized that in mammals the lower jaw was a single bone on each side which articulated with the squamosal bone of the skull, whilst in reptiles the lower jaw was made of several bones one of which, the articular, moved on a quadrate bone which was part of the skull.

By 1820, Meckel showed that the mammalian malleus first appeared as the hinder part of "Meckel's cartilage" and corresponded with the reptilian articular, and by 1818, C. G. Carus had suggested that the incus is the quadrate.

In 1837, Reichert gave a connected account of the development of the visceral arches in mammals and birds, adopting Carus' and Meckel's suggestions, and the whole story is now commonly known by his name.

The great difficulty in envisaging intermediates between the modern reptile and the mammalian condition led to many alternative suggestions, so that the publication by E. Gaupp (1913) of an exhaustive treatise on the problem which established, by a consideration of all then available lines of evidence, the fact that the old reptilian jaw articulation was represented in mammals by that between the incus and malleus, was important. An admirable account of the whole matter will be found in E. S. Goodrich, "Studies on the Structure and Development of Vertebrates," London 1930, chapter VIII.

The Ear in Modern Reptiles and Mammals

It follows from the foregoing that the problems to be met in the discussion of the evolution of the mammalian ear involve a knowledge of the conditions in recent reptiles and mammals and a discussion of a series of fossil reptiles leading up, if not to a mammal, to a mammalian structure.

It is certain, not only from the adult structure, but from careful investigation of the mode of development, that the sound transmitting apparatus, the quadrate and the articular of all living reptiles and birds, conform to a single fundamental pattern.

In this there is a tympanic membrane separating a tympanic cavity, formed by outgrowths of the hyoid cleft, from the outer air. This membrane lies behind the quadrate and in front of the musculus depressor mandibuli, above the retroarticular process of the lower jaw. It may, as in

Chelonia, be spanned across a deeply notched hinder border of the quadrate, or as in Crocodilia, lie at the extreme dorsal and anterior end of the quadrate far removed from the lower jaw, or it may, as in lizards, lie attached to the back of an almost vertical quadrate below the end of the paroccipital process or rather of a squamosal attached to it.

Thus the tympanic membrane may be attached to the supratemporal, squamosal, quadratojugal, quadrate, angular, and articular bones, or any one or combination of them. The tympanic membrane may be lost as in *Sphenodon* and snakes.

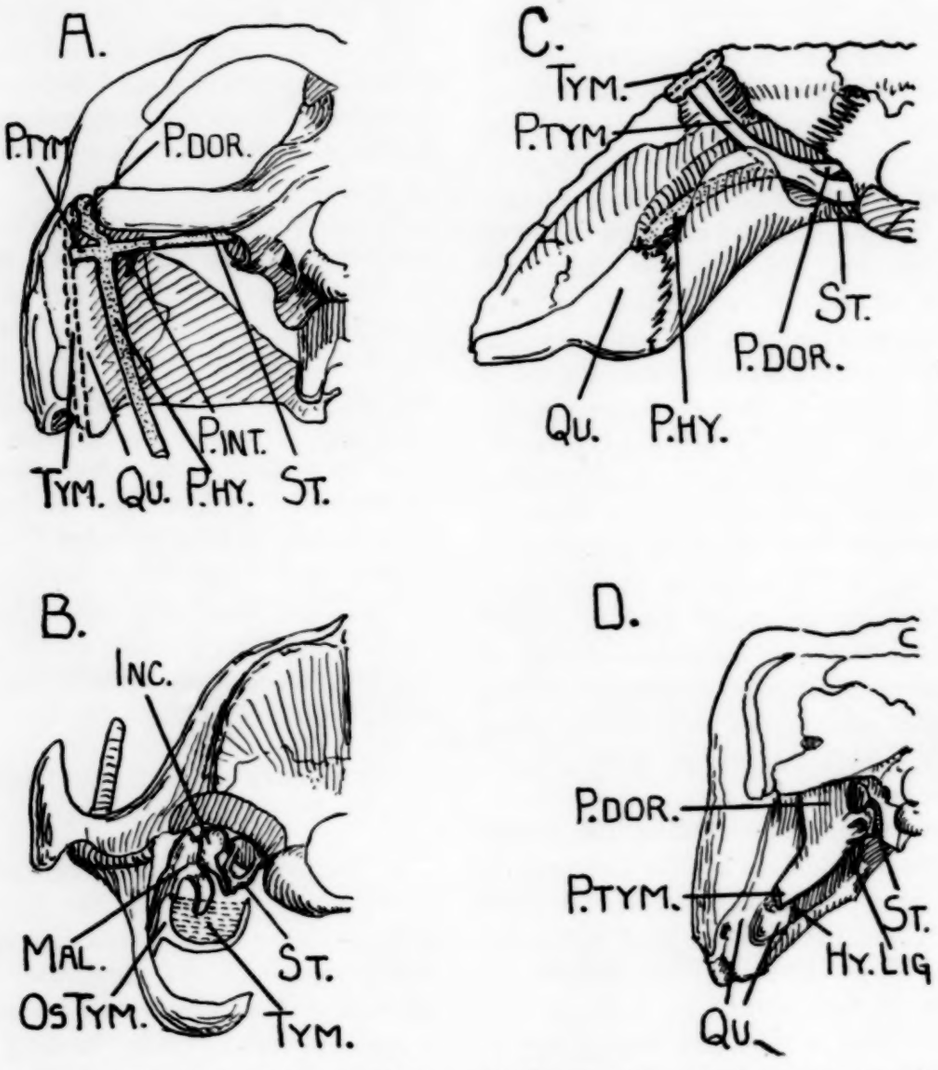


FIG. 1. Diagrams of the sound transmitting apparatus of four animals: A, bird-like reptile (essentially lizard). B, mammal (essentially young marsupial). C, Labyrinthodont amphibian (*Rhinesuchus*). D, mammal-like reptile (*Dimetrodon*).

HY. LIG., ligament in *Dimetrodon* representing the hyoid process of a labyrinthodont stapes; INC., incus; MAL., malleus; OS TYM., tympanic bone of mammal; P. DOR., processus dorsalis of stapes; P. HY., processus hyoideus of stapes; P. INT., processus internus of stapes; P. TYM., processus tympanicus of stapes; QU., quadrate; ST., stapes near the footplate; TYM., tympanic membrane.

The vibrations of the tympanic membrane are transmitted to the membrane that closes the fenestra ovalis by a straight rod composed of two parts and bearing a number of processes (cf. fig. 1, A). The

rod is, during embryonic development, a single blastema of tight-packed mesenchyme, in which two centers of chondrification arise: one proximally, a straight rod whose expanded footplate fits into the fenestra ovalis (fig. 1, ST), the other, the "extracolumella," which is attached to the proximal element and is by an expansion of its lateral end (P. TYM.) embedded in the tympanic membrane. Later in development the proximal part of the apparatus ossifies, the point of separation of this bone from the extracolumella perhaps not being the same as the original meeting point of the two cartilages. Very rarely this bone is perforated by a foramen through which passes an artery.

From the columella, mesial of and entirely detached from the tympanic membrane, a dorsal process (P. DOR.) of cartilage formed from a special centre passes up to be attached to the outer end of the paroccipital process (here entirely opisthotic) and to the supratemporal or squamosal which overlies it. This process becomes detached except for a ligamentous connection from the extracolumella in most adults.

From the extracolumella, lateral to the dorsal process, another cartilaginous rod arises which passes downward to become continuous with the hyoidian cartilage which passes forward below the mouth to support the tongue. This cartilaginous string, the "hyoid process" (P. HY.), may remain complete as in *Sphenodon*, or it may fuse with the articular as transiently in crocodiles, or it may be tied down to the back of the quadrate as in tortoise embryos.

In some forms (lizards and snakes) an additional process of the extracolumella grows forward above the tympanic cavity to rest upon the inner surface of the quadrate. This is the processus internus of the extracolumella.

In mammals (fig. 1, B) the conditions are entirely different. There is a tympanic membrane which during development lies ventral and lateral of the hinder end of Meckel's cartilage, which in reptiles forms the articular bone, and this membrane is spanned across a horse-shoe shaped bone, the "tympanic" (OS TYM).

This membrane is attached to the outer (lower in actual position in most embryos) surface of a special process of the hinder end of Meckel's cartilage, which passes inward, downward and forward, so that its tip lies in the centre of the tympanic membrane. Ultimately this cartilage fuses with a membrane bone the goniale or prearticular, and ossifies to form the malleus, to which is attached a muscle, the m. tensor tympani, which is innervated by the fifth cranial nerve.

The malleus is supported by articulating with the incus, a small bone attached to the squamosal by a ligament or its equivalent, which, in turn, has an articulation with the distal end of a stapes whose proximal end is buried in the membrane closing the fenestra ovalis. The stapes is slung up to the roof of the tympanic chamber by a stapedial muscle innervated by the seventh cranial nerve, and attached usually to a special small process, "dorsally" directed, immediately proximal to the articulation of the stapes with the incus.

The stapes is usually perforated by a hole through which passes a stapedial artery to the orbit.

It is evident that this very great difference between the sound-transmitting apparatus of the middle ear of mammals and that found in living reptiles may be brought into relationship with the fact that the mammalian jaw is a single membrane bone, which articulates with a squamosal, also a membrane bone, whilst the modern reptile has a complex lower jaw. This includes an articular bone ossified in the hinder end of Meckel's cartilage, surrounded by a series of membrane bones, the articular moving on a quadrate, also a cartilage bone which is connected to the braincase by a series of membrane bones.

The homology (in a wide sense) of the structures concerned having thus been safely established by Gaupp and Goodrich, it remains to consider how the changes of function which have occurred can have

taken place during the continuous process of the evolution of mammals and birds.

The History of the Mammalian Ear

The existing fossil evidence which concerns mammalian ancestry is immense in amount but to a very large extent the materials have not yet been adequately prepared or described. None the less it is possible to pick out a series of animals which, placed in their order of time, show a continuous story of change for each part of the body as they are followed from the beginning to the end of the story. The series is as follows.

Stage 1.	Labyrinthodont amphibian	Carboniferous
2.	Captorhinomorph reptile	L. Permian
3.	Pelycosaurian	L. Permian
4.	Deinocephalian	M. Permian
5.	Gorgonopsid	U. Permian
6.	Procynosuchid	U. Permian
7.	Cynodont	L. Trias
8.	Ictidosaurian	U. Trias
9.	Ictidosaurian *Oligokyphus*	L. Jurassic

The ear in amphibians and early reptiles: It is convenient to begin with an Upper Permian labyrinthodont, *Rhinesuchus,* from South Africa. The head of such an animal, which was at any rate largely aquatic, is flattened, the skull being only about as deep as the lower jaw, and the total height at the back of the head being much less than its width (see fig. 1, C).

The quadrate condyle is cylindroid and lies quite posteriorly at the hinder and lower end of a wedge-shaped cheek. The bone rises forward, its upper and posterior surface being covered mesially by the pterygoid and laterally by the quadratojugal and squamosal, so that a triangular area directed upward and backward remains visible. The summit of this triangle is usually roughened for some ligamentous attachment; beyond this point the palatoquadrate is continued in cartilage to join the ventral part of the epipterygoid and so to continue (as Säve-Söderbergh showed) to the anterior end of the palate. The squamosal continues forward, sheathing the quadrate by an internal flange which passes abruptly into the outer surface of the skull. This surface ends at a border which turns down to form half of the "otic notch" which is completed by the supra-temporal and tabular bones. The tympanic membrane is stretched across the notch.

The tympanic cavity floor rests in a groove (first described by Sushkin, 1927) received in the posterior surface of the quadrate ramus of the pterygoid.

The stapes is a slightly bent rod of bone which ends proximally at a truncation which was attached to the membrane covering the fenestra ovalis. From some point, which may be ventral as in *Eryops,* or may be anterior in position as in most later capitosaurines, there arises from the proximal end of the stapes a process, separated by a notch from the foot-plate, which articulates with and may be attached by suture to some part of the border of the fenestra ovalis, in later forms usually to the proötic.

The stapes is often so held in its natural position, when it passes outward until its end lies in the middle of the tympanic notch, usually so nearly flush with the ridge that gives attachment to the membrane that it is obvious that there was no considerable cartilaginous extension. In many genera of Upper Permian and Triassic labyrinthodonts the lower surface of the stapes, just lateral to the stapedial foramen, bears an attachment (first pointed out by Parrington, 1948) which takes various forms. It may be a deep, rather narrow groove ending in a steep face proximally whose floor lacks perichondral bone whilst the sides are continued by flanges of periosteal bone round the base of a cartilaginous process; or the pit may be floored by perichondral bone; or there may be an outstanding process.

In every case the process must have passed outward, lying on the floor of the tympanic chamber, in the groove in the pterygoid, and have ended by being tied down to the attachment on the quadrate

which lies at the end of that groove. I suggested in 1926 that this arrangement must have occurred in the Upper Carboniferous and Namurian loxommids, and there is no evidence that it did not do so, and now much that it did.

We therefore have in these labyrinthodonts a stapes which effectively reproduces the whole columella apparatus of a bird-like reptile: it has a footplate, a process to the proötic comparable to the dorsal (intercalary) process, a ventral process to the hyoid, and a processus tympanicus. All that is missing is the internal process to the quadrate which is in any case of inconstant occurrence. It would be natural now to consider the reptile *Captorhinus,* which though a contemporary of pelycosaurs is itself a late member of the ancestral group of cotylosaurs.

But the best-preserved materials are of *Dimetrodon,* where the conditions have been well described and figured by Romer and Price (1940) (see fig. 1, D). Here the fenestra ovalis is a hole which is surrounded by well-marked articular faces on the paroccipital and proötic, cartilaginous projections from which bones are supported by processes of the basioccipital and basisphenoid. The large opening of irregular shape is fitted by an enlarged footplate of the stapes which has a smooth concave surface toward the perilymph and a broad (sometimes 5 mm. wide) belt for articulation with the lips of the fenestra.

This footplate projects directly inward when in natural position and is connected by a neck (through which passes a foramen for the stapedial artery) with the distal part of the bone, which is deep and narrow, lying against but not actually touching the posterior and admesial surface of the quadrate ramus of the pterygoid and the quadrate. The nearly straight upper edge of the proximal part of this region of the stapes is firmly attached to a special ridge on the lower border of the proötic, in front of the groove on the paroccipital process which is the limit of a tympanic cavity. This attachment may be 24 mm. long with a width varying from 3 to 5 mm. in a small stapes appropriate to a skull about 25 cm. in length.

The ventral border of that flat face of the stapes which lies parallel and near to the quadrate and pterygoid bears a very pronounced area, deeply incised proximally, for the attachment of a ligament. This begins above the pedicel of the head and extends to within a couple of millimetres of that lateral end of the bone which is continued in cartilage, perhaps for a few millimetres, to rest in a pit on the inner surface of the quadrate, a little above the condyle. This pit is really the end of a groove with a marked upper border on the quadrate. The ligament can only have been attached to the ventral part of the pterygoid process of the quadrate and to the pterygoid which is attached to it, where the two bones form an inwardly directed flange which may well have marked the lower limit of the tympanic chamber. Thus the quadrates in a specimen in the Museum of Comparative Zoology (MCZ 1632) show a well-marked sculpturing for the attachment of this ligament and for the end of the stapes in these places. This depression in the two bones may be called the stapedial recess.

In *Ophiacodon* (fig. 2A) the stapes differs from that of *Dimetrodon* in having an even larger footplate and in the dorsal process having a much shorter attachment to the proötic, and lying nearer to the footplate. The stapedial recess is so greatly exaggerated in *Ophiacodon* that the suggestion that it housed a tympanic cavity is strengthened but it is obvious that there can have been no tympanic membrane, for the cartilage-coated extremity of the stapes is directed into a deep hole from which there is no exit in any appropriate direction.

I have already (1948) pointed out that there is no place where a tympanic membrane could have been placed in *Dimetrodon,* and indeed it is very difficult to believe that a stapes so powerfully connected to the fenestra ovalis, to the proötic, and to the quadrate and pterygoid as in the

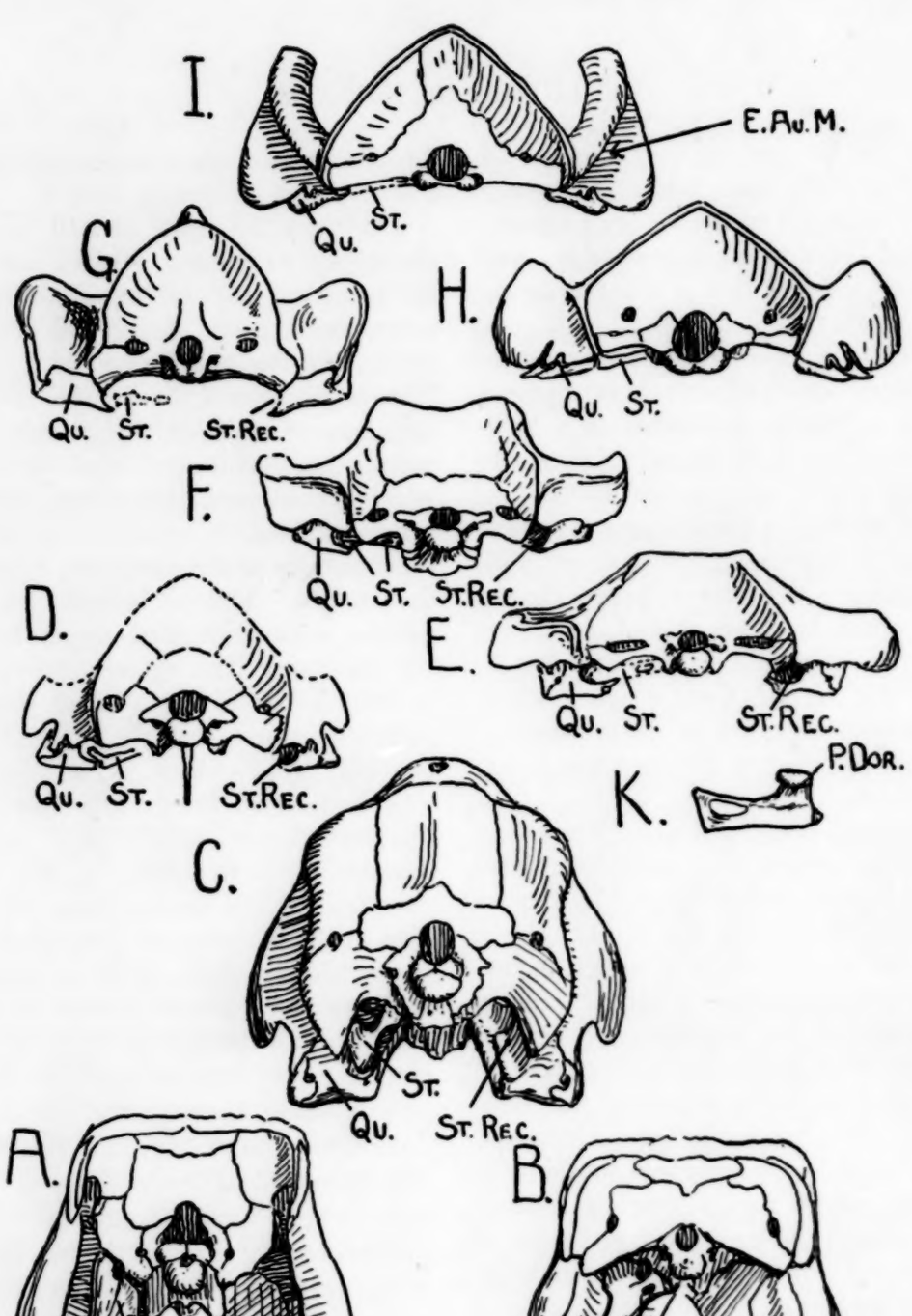


FIG. 2. Occipital views of a series of mammal-like reptiles, the oldest below, the most recent above. To show that the stapes of the later animals is the morphological equivalent of that of pelycosaurs. A, pelycosaur, *Ophiacodon,* L. Permian; B, pelycosaur, *Dimetrodon,* L. Permian; C, deinocephalian, *Ulemosaurus,* L. M. Permian; D, therocephalian, *Lycedops,* U. M. Permian; E, gorgonopsid, genus uncertain; L. U. Permian; F, gorgonopsid, "*Scylacops,*" U. Permian; G, procynosuchid, *Leavachia,* U. Permian; H, cynodont, *Thrinaxodon,* Basal Trias; I, cynodont, *Diademodon,* L. Trias. A and B after Romer and Price, 1940; C after Efremov, 1940; D after Broom, 1936; E and H after Parrington, 1946; F after Watson, 1951; G after Broom, 1948; I after Watson, 1911.

K, left stapes of the gorgonopsian "*Scylacops*" from in front, from a drawing by Parrington.

Reference letters:—E. AU. M., external auditory meatus; P. DOR., processus dorsalis of the stapes; QU., quadrate; ST., stapes; ST. REC., stapedial recess on quadrate and pterygoid for attachment of the outer end of the stapes.

case in that genus could have been actuated by a tympanic membrane.

It has long been known that the stapes of *Captorhinus* is comparable to that of a pelycosaur, and Price (1935) showed that they are indeed very similar; even a roughening for the ventral hyoidean ligament is shown in materials of *Captorhinus* and *Labidosaurus* in Harvard. Thus the *Dimetrodon* condition is typical of early mammal-like reptiles in general.

It is furthermore evident that the pelycosaur stapes is homologous with that of a labyrinthodont: it is a rod of bone with a footplate in the fenestra ovalis, a dorsal process articulated with the proötic, a hyoid process (represented by a ligament) to the quadrate, and a processus tympanicus directed toward a tympanic membrane which has vanished.

It has already been shown that the labyrinthodont stapes represents the whole sound-transmitting apparatus of a bird-like reptile, and it therefore follows that that of the early mammal-like reptile has the same morphological value. It is therefore irrational to look for extensions of the pelycosaur stapes which can be homologized with various processes of bird-like reptiles.

The ear in later mammal-like reptiles: It is now necessary to trace the fate of the stapes in later mammal-like reptiles (fig. 2). The history of these animals has a gap after the pelycosaurs, of not very great length, and then continues in "the copper-bearing sandstones of the Urals" in the primitive Deinocephalia, *Deuterosaurus* and *Brithopus*. The stapes of these reptiles are unknown, but fortunately those of their successors *Ulemosaurus* and *Titanosuchus* are well preserved and the former described. They are reptiles with very large massive skulls, easily comparable with pelycosaurs, from which they differ by an enormous increase in size and massiveness of the paroccipital processes, which are turned downward to give very powerful direct support to the squamosal and quadrate.

In *Ulemosaurus* Efremov (1940) has figured a stapes in position. It is a short rod with a somewhat expanded base which widens distally into a "leaf shaped" structure whose dorsal part seems to be fitted to the lower surface of the outer part of the paroccipital process, whilst the more massive lower end lies in contact with the floor of a deep stapedial recess. It is evident that the bone can never have come into contact with a tympanic membrane. It is very similar in general shape to that of *Dimetrodon,* but lacks the foramen for the stapedial artery.

It is evident that the stapes includes all the parts of the pelycosaur stapes, which we saw to be homologous with the whole sound-transmitting apparatus of a lizard.

Titanophoneus, a titanosuchid contemporary of *Ulemosaurus,* has a stapedial recess in its quadrate, quite like that of *Dimetrodon.*

The Deinocephalia were followed by other groups, the Therocephalia and Gorgonopsia, which are in effect derived from them. From the lowest zone of the South African Karroo, which is a little more recent than the Russian beds containing *Ulemosaurus,* Broom (1936) has described the therocephalian *Lycedops.* Here the paroccipital processes project outward nearly horizontally, and the quadrate is much smaller relatively than in Deinocephalia. Broom draws two fragmentary stapes as they are shown on a weathered face; each has part of a dorsal process (identified as extracolumella). This projects into what is clearly a stapedial recess lying above a hook-shaped lower and inner extremity of the quadrate, the deeper part of the recess being represented by a bony wall, interpreted by Broom (1936) as opisthotic, which seems impossible. It is probably the hinder end of the quadrate ramus of the pterygoid.

The Gorgonopsia from the two highest zones of the Permian of South Africa includes a very large number of animals which seem to agree with E and F of figure 2. In these the stapes (K, fig. 2) seems to have a flattened shaft arising from a plug-like footplate, with a large

foramen for the stapedial artery. The bone, very near its distal end, bears a dorsal process which articulates with the distal part of the paroccipital process and holds the ventral surface of the distal end of the stapes in contact with the ventral part of a deep stapedial recess in the quadrate. The stapes ends in a face continued in cartilage, the whole of which seems to have lain within the recess. Broom (1948) has drawn the occiput of the primitive cynodont *Leavachia* (G, fig. 2) as it is shown after a superficial preparation. It seems evident that the concave notch in the inner border of the quadrate implies the existence of a stapedial recess.

The early true cynodont *Thrinaxodon* from the basal Trias shows a different condition, well described by Parrington (1946) (fig. 2H). Here the stapes is a short flattened bone with a rounded head which fills the bowl-shaped mouth of the fenestra ovalis. The bone is perforated by a large foramen and from its extreme distal end a very slender dorsal process rises toward (or to) the paroccipital process. The distal end of the bone was continued by cartilage, and part of its area lies entirely behind the quadrate, with the abruptly truncated inner surface of which the remainder of the cartilage must have articulated. It is evident that the stapedial recess is no longer developed, the stapes at last gaining a direct end-on abutment on the quadrate.

Parrington figures the stapes of a much later cynodont (*?Trirachodon*) in which the distal end is much more completely ossified than in *Thrinaxodon*, and is evidently divided into an abutment for the quadrate and a short process passing behind that bone to be inserted into a tympanic membrane.

In *Diademodon* (*Gomphognathus*) (I, fig. 2) the stapes is incompletely known but the well preserved quadrate shows that there is no stapedial recess, but that the quadrate bears a special face directed toward the fenestra ovalis.

In *Diademodon* a deep notch, associated with the arrangement of muscles, cuts down into the squamosal so as to separate that part which is attached to the parietal and tabular from the zygomatic part of the bone. At the meeting point of these rami the bone is rigidly attached to the end and a little to the front face of the paroccipital process, a deep crest on its occipital surface dying out at the level of the lower surface of the end of the paroccipital process.

The outer surface of this crest can be followed upward into the border of a deep groove facing outward on the admesial edge of the zygomatic part of the squamosal. This groove extends forward to end on the outer surface near the summit of the head.

W. K. Gregory (1910) claimed that this groove housed an external auditory meatus, and this view has been generally accepted. That it is true is shown by two new facts: the description by Parrington (1946), in an unnamed Middle Triassic cynodont, of a special bony funnel at the lower end of this groove ending abruptly at "a smooth, slightly expanded, rounded lip" which may well have carried a tympanic membrane; and the conditions found by Kühne in the tritylodont *Oligokyphus*, where the same groove not only extends far forward toward the eye, but is so deeply enclosed by the infolding of its borders that it can only have housed a tube 2–3 mm. in diameter, lying exactly in the position of the cartilaginous tube which is the external auditory meatus of the monotreme *Ornithorhynchus*. Thus *Diademodon* certainly had a tympanic membrane, a tympanic cavity, and some arrangement whereby the vibrations of the membrane could have been transmitted to the stapes, in fact, the extension of that bone found by Parrington in his Middle Triassic cynodont.

Thus *Diademodon* certainly, *Cynognathus* and *Thrinaxodon* with great probability, possessed a tympanic membrane at the inward end of a meatus which lay in a groove on the posterior surface of the squamosal, lateral to and above the quadrate.

But the Deinocephalia and earlier reptiles lacked a membrane and external auditory meatus. None the less they and most other "therapsids" possess a back-standing ridge from the tabular and squamosal, which lies immediately lateral to the end of the paroccipital process, corresponding exactly in position to the ventral end of the inner wall of the meatal groove in *Diademodon*. Indeed in some gorgonopsids (cf. fig. 2, F) there is a depression crossing the hinder surface of the squamosal which recalls the hinder end of the meatus in *Cynognathus*.

In Deinocephalia, where this crest first appears, it is best known in *Ulemosaurus* where the squamosal bows outward from the quadratojugal to house a great masseter muscle. It thus acquires a posteriorly directed surface lying lateral to the tabular and the area of insertion of the neck muscles, extending down over the paroccipital process. This "new" surface is bounded on its inner side by a rounded groove, lying almost entirely in the squamosal. The groove ends behind the quadrate immediately above the retroarticular process of the lower jaw, and it seems certain that a large musculus depressor mandibuli occupied the groove and some part of the rest of the hinder surface of the squamosal.

Thus, this groove, completely filled by muscle, is most unlikely to have housed also a meatus, and the shapes of all the structures concerned seem to make it clear that there was no tympanic membrane.

Somewhere between *Ulemosaurus* and *Diademodon*, we have to envisage the introduction ***de novo*** of a tympanic membrane. Whether or not this means that the tympanic chamber, an air-filled space connected with the pharynx by the eustachian tube, was lost and regained is uncertain.

In *Dimetrodon* the shape of the lower surface of the paroccipital process with its groove and posterior ridge suggests that a chamber was still extant. In most Deinocephalia it may well have been absent, but in some gorgonopsids and therocephalians the nature of the lower surface of the paroccipital process suggests that it still survived, *e.g., Arctops* (Watson, 1914, 1921). In *Diademodon* it evidently existed.

It is thus in no way unlikely that a tympanic cavity existed continuously in some lines of mammal-like reptiles, even after the loss of a tympanic membrane; conduction of sound waves through bone may have been more satisfactory if the stapes was hung up in air.

In later mammal-like reptiles the retroarticular process of the articular, to which the m. depressor mandibuli was attached, vanishes, and the muscle can no longer have functioned and must have been lost, the mouth having been opened by some device analogous to the monotreme detrahens mandibuli, or mammalian digastric.

Thus the ridge made by the squamosal and tabular can only remain as a limit to the insertion of the neck muscles, the vertical groove on the squamosal lateral to it having no infilling. Its apparent diversion to the outer side of the head, dorsally, is apparently a secondary result of the back-turning of the posterior border of the temporal fossa to lengthen the masticating muscle which arose from it.

Thus there is no evidence to show whether *Leavachia* did or did not possess a tympanic membrane. The apparent presence of a stapedial recess in this animal suggests that it did not, agreeing with its contemporary cynodonts *Cynosuchus* and *Permocynodon*. The only possible position for a tympanic membrane in *Diademodon* is immediately lateral to the paroccipital process attached above to the squamosal where Parrington's specimen suggests that the external meatus ends. This is essentially where the membrane is placed in figure 7.

The Lower Jaw and Quadrate

Stages in evolution: The next matter to be considered is the series of changes in the lower jaw and quadrate which lead up to the mammalian condition.

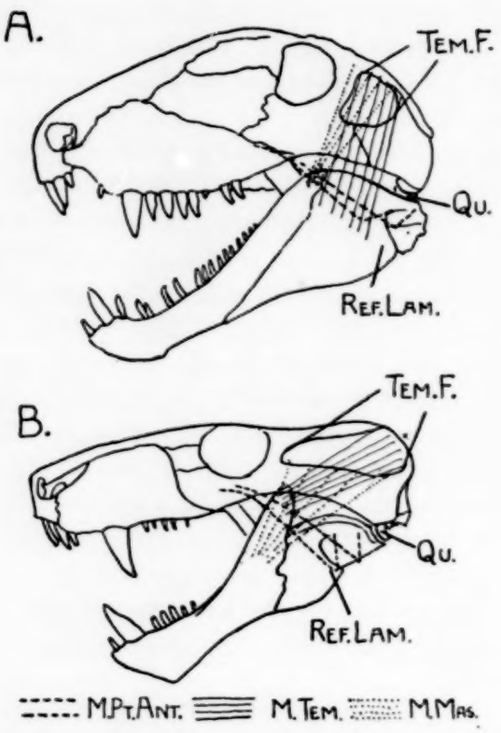


FIG. 3. Lateral views of the skull and lower jaw of A, the pelycosaur *Dimetrodon*, and B, a gorgonopsid, to show the probable origin and attachment of certain muscles.

REF. LAM., reflected lamina of the angular; TEM. F., temporal fossa; QU., quadrate; M. PT. ANT., anterior pterygoid muscle; M. MAS., masseter muscle; M. TEM., temporal muscle.

These parts of the skull are an important element of the feeding apparatus, and must perform this function throughout the whole history of mammal-like reptiles. The shapes and sizes of all parts of the jaw apparatus are determined by the nature of the animal's food, the way in which it is caught or bitten off, and the preparation it undergoes before being swallowed.

The jaw apparatus of *Dimetrodon* is very well known from the work of Romer and Price (1940), and I (1948) have discussed its musculature and possible movements. The animal is large (skull length 140–420 mm.) with very powerful conical teeth in the premaxilla and anteriorly in the maxilla. It was certainly rapacious, killing large prey by biting.

The lower jaw is narrow from side to side but deepened posteriorly to gain girder strength.

The temporal muscles arise from the lower surface of a flat skull roof and pass directly downward to the lower jaw; part (an incipient masseter) is inserted on the extreme hinder end of the dentary, the remainder on the inner surface (figs. 3 and 4). In order to allow the mouth to be opened sufficiently to allow the "canine" teeth to separate enough to span a reasonable animal as prey, the long muscles lie in a short temporal region and the skull is very deep, the quadrate condyles lying very far below the base of the brain. Two pterygoidal muscles are attached to the hinder part of the lower jaw: the external pterygoid arising from the epipterygoid bone is inserted on a special process of the articular and the anterior pterygoid, with an origin on the dorsal surface of the palate, ends by rolling round the lower border of the angular at the hinder part of the jaw and passing up its lateral surface to be attached high up.

The angular bone is thus notched and a "reflected lamina" stretches back outside the hinder part of the muscle to end freely. In order to allow the temporal muscles to thicken during their shortening, a window, the "temporal fossa," is cut out of the nearly vertical side wall of the temporal region (Gregory and Adams, 1915).

In the next stage, represented by the

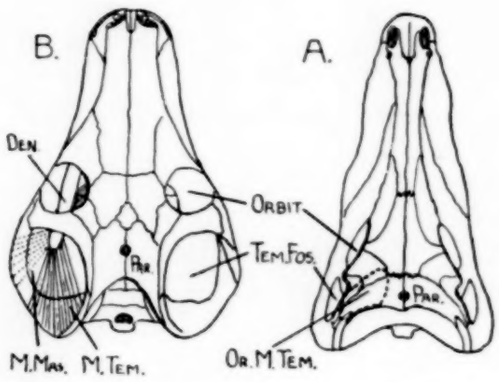


FIG. 4. Dorsal views of the skulls of A, the pelycosaur *Dimetrodon*, and B, a gorgonopsid.

DEN., the dentary bone of the left lower jaw; M. MAS., masseter muscle; M. TEM., temporal muscle; OR. M. TEM., the area of origin of the masseter and temporal muscles; TEM. FOS., the temporal fossa; PAR., the parietal.

early Russian Deinocephalia, the skull remains high, the quadrate of *Deuterosaurus* still being a large bone, supported on its inner side by a down-turned paroccipital and a relatively deep ramus of the pterygoid. But the temporal fossa is enlarged, its upper end cutting into the outer side of that flat cranial roof from which in pelycosaurs the temporal muscles arise, in such a way that the origin of some part of the muscles is from the now free upper border of the squamosal. And similarly the lateral part of the muscle, the masseter, moves outward a little along the squamosal border. (Cf. shape of lower border of fossa of *Ulemosaurus,* Efremov (1940), fig. 1.) But in other respects *Deuterosaurus* greatly resembles *Dimetrodon.*

The next stage is represented by the older Russian titanocephalids. In them the temporal fossa increases in size, and the hinder part of its border is pulled backward so that muscles attached to it pass downward and forward to the dentary at a low angle to the horizontal. The zygomatic arch may be so narrow that it can scarcely have served as an attachment to the masseter muscle. The quadrate becomes less high and the quadrate ramus of the pterygoid further reduced. The paroccipital process now powerfully supports the squamosal and quadrate.

In the next stage, the Gorgonopsia, further changes go on in the same general direction (figs. 3 and 4).

The temporal fossa is increased in size by the further extension backward of the hinder border of the squamosal, and by an outpushing of the zygomatic part of the squamosal to house a masseter muscle whose attachment has moved further down the dentary, but which still arises posteriorly from the squamosal. These changes cause the temporal muscles to pass forward nearly horizontally, and necessarily go on *pari passu* with an elevation of their point of attachment to the jaw above the line joining the tooth row to the jaw articulation. This attachment is onto the dentary, and this bone develops an upward and backwardly directed process which stands out freely above the upper border of the surangular.

The pterygoidal muscles retain their original positions, the anterior pterygoid muscle pulling the hinder part of the jaw forward and rotating it upward on the quadrate, whilst the temporal muscles pull the summit of the dentary backward and hence by a bell-crank lever close the mouth.

Thus the quadrate serves chiefly to transmit pressures from in front directly to the squamosal in whose front face it lies, and thence to the paroccipital.

The quadrate thus becomes reduced in height, and with the quadratojugal attached to its lateral border, lies in a hollow in the lower part of that transversely placed sheet of squamosal which is attached to the paroccipital and, some distance lateral to the quadratojugal, turns forward to the zygoma.

The quadrate is held in its recess by a quadrate ramus of the pterygoid, which passes mesial to it in the ordinary way, and by a special quadrate ramus of the epipterygoid which may reach the quadrate and ultimately pass in front of it.

It is evident from consideration of the whole material of "theriodonts" that that group contains members of many lines of descent pursuing parallel tracks (see Olson, 1944). One of these is an increase in the size of the dentary by enlargement of that upstanding process to which the temporal muscles are attached. As this pushes its way upward, the hinder part of the jaw decreases in size, becoming more slender, until it becomes converted into a narrow rod of surangular, angular, and prearticular bones received in a groove in the greatly enlarged hinder part of the dentary and held in place by a splenial and coronoid on the inner side.

This rod ends behind in the articular bone, whose truncated hinder end is the articular face, the bone often retaining a ventral process for the attachment of the posterior pterygoid muscle, but having no retroarticular part at all.

Ultimately the dentary grows back in contact with the upper surface of the sur-

angular, until it very nearly reaches the articular face of the quadrate, failing to do so only by some two or three millimetres in a skull 130 mm. in length.

Just as the coronoid region of the dentary grows upward and backward above the upper surface of the hinder part of the jaw in theriodonts, so the lower border of the dentary where its suture with the angular reaches the lower border of the jaw becomes a muscle insertion and, presumably to improve the direction of pull of muscles attached to it, grows downward until it comes to lie far below the hinder part of the jaw. In the earliest cynodonts, *Permocynodon* and *Leavachia*, it is uncertain whether this detachment has begun; in *Thrinaxodon* it probably is incipient; in *Cynognathus* and all its contemporaries it has gone so far that the hinder part of the jaw is in effect merely lying in a groove, half way up the inner surface of the dentary (fig. 5). For the greater part of its extent it is fully exposed from within, and much of its outer surface is free, the longest contact being along the upper border.

It is evident that the relation of the two parts of the jaw to one another is such that the forces applied to it by the pull of muscles must be so directed that they do not tend to bend the jaw, but merely force the dentary backward along the direction of the hinder part of the jaw.

The forces so transmitted may well have been large for there is little evidence that the area of the articular surface of the quadrate is greatly reduced until a very advanced stage of the process. But the quadrate and its attached quadratojugal are reduced in height in such a way that very nearly the whole of their posterior surface becomes supported by the squamosal. This change has an obvious functional meaning: it transmits heavy pressures nearly directly to the powerful paroccipital process, and excludes any possibility of the quadrate being "rocked" in its recess in the squamosal.

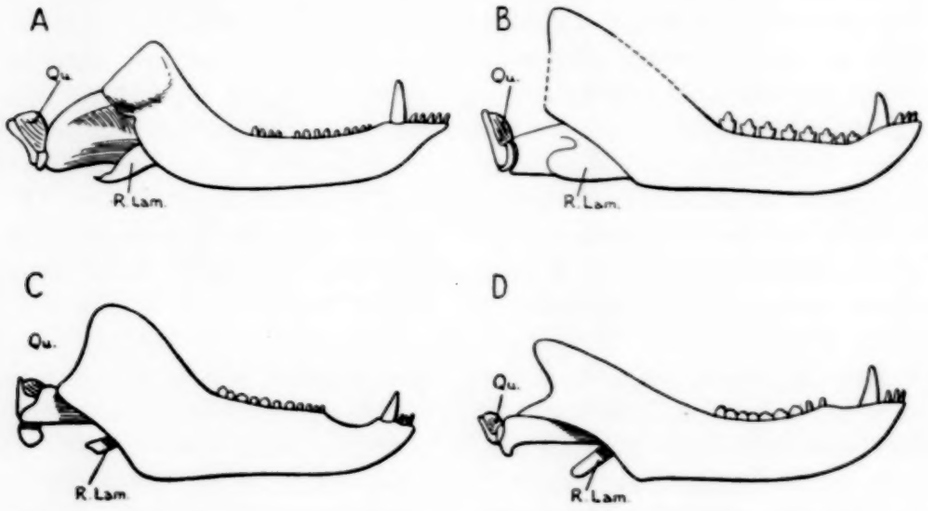


FIG. 5. Right lower jaws with a somewhat diagrammatic quadrate and quadratojugal of the correct height. A, *Permocynodon, Cisticephalus* zone, Russia; after Suskin and Kouzhukova. B, *Thrinaxodon, Lystrosaurus* zone, South Africa; after Parrington. C, *Gomphognathus* sp., *Cynognathus* zone, South Africa; original. D, *Protacmon, Cynognathus* zone, South Africa; original.

But this shortening seems to be part of a general process in theriodonts whereby all structures which lie below the base of the hindbrain and behind the transverse flanges of the pterygoids tend to be reduced in height. Thus the basioccipital part of the condyle is pinched out to isolate two mammal-like exoccipital condyles, the tubera basisphenoidales are reduced to

slender ridges, and the quadrate rami of the pterygoid and epipterygoid are so "eroded" ventrally, that by the stage of *Cynognathus* the pterygoid is cut short at the basipterygoid process; and independently, *Cynidiognathus* and *Protacmon* arrive at a condition in which the quadrate ramus of the epipterygoid is similarly cut short, and the quadrate lies entirely "free" in its depression on the front face of the squamosal. In a skull some 130 mm. long, it and its attached quadratojugal are 12 mm. wide and 9 mm. high, figures small for a bone providing the whole articulation for a lower jaw, but large compared with a mammalian incus.

The cynodonts are in effect ancestral to the Ictidosauria, of which the best known member is *Oligokyphus* from the Lower Lias of England. Dr. W. G. Kühne has completed a description of this animal which will be published by the British Museum in due course. In this animal Kühne has shown: that the wear on the teeth implies a propalinal movement of the lower jaw; that the lower jaw has a cynodont-like hinder region lying attached to a groove in a dentary which does not quite reach the squamosal; that there seems no possibility of movement of the dentary on the surangular: that therefore the lower jaw can only move backward and forward if the quadrate be movable.

The area of squamosal to which the quadrate must be attached in *Oligokyphus* and in the more primitive allied *Bienotherium* is a largely horizontal surface, which may really represent the upper part of that depression on the anterior face of the squamosal in which the quadrate of a cynodont rests, the hinder wall with its two notches having vanished. It is evident that these changes in the mode of articulation would enable the quadrate to move. In fact, the quadrate of *Oligokyphus* is known; it is difficult to compare it with that of a cynodont, but the whole bone in a skull some 90 mm. long is only about 4 mm. high and wide, not greatly bigger than the incus in some mammals.

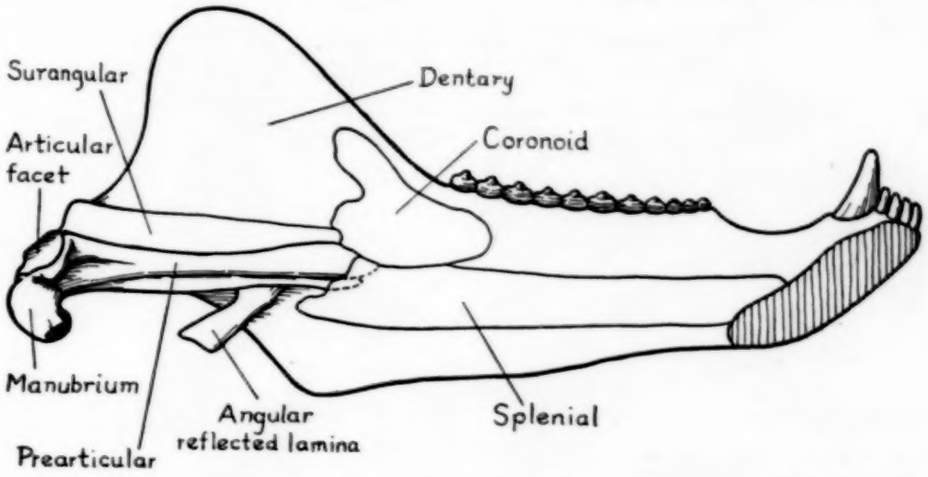


FIG. 6. *Gomphognathus*, inner surface of a left lower jaw, to show the great reduction of the hinder part of the jaw and its relationship to the dentary (after Watson, 1951, reproduced with permission of Yale University Press).

Thus the process of reduction in size of the quadrate and of the structures which hold it rigidly in place is a long one; it proceeds regularly in the theriodonts from an early stage in the history of the group to the time in the lower Lias when it was, so far as we know, represented only by a single "family," dying out a little later after the time of the Stonesfield slate.

The angular notch (fig. 5 and 6[1]): We must now return to consider the angular and its notch and reflected lamina (Watson, 1912). The notch in *Dimetrodon* serves to isolate a straight ventral border of the

[1] After Watson 1951.

hinder part of the lower jaw around which the hinder end of the anterior pterygoid muscle can pass to its attachment on the outer surface. The arrangement allows the ligament to slide to and fro over the lower surface, thus enabling the muscle, during contraction, to close the mouth and slide the jaw forward. The hinder part of the lower jaw in front of the notch must remain deep, in part no doubt to give girder-strength to the structure, and in part to give attachment to inter-mandibular muscles which are functionally necessary. The reflected lamina serves to carry the attachment of these muscles farther back.

The notch and lamina can be found in every "therapsid" reptile: sometimes the notch is long and the muscle has an extensive attachment, sometimes it is small. The reflected lamina is always present, the space between its inner surface and the body of the bone being often only just wide enough to house the sheet of tendon in which the muscle ends, but sometimes expanded into a great pocket, which may conceivably have housed a gland.

In the pro-cynodonts *Permocynodon* and *Leavachia* the reflected lamina differs in no way from that of gorgonopsids, and in the early cynodonts it seems generally to have retained the same form.

But in the later cynodonts where the "angle" of the dentary extends well below the hinder part of the jaw the reflected lamina attains a remarkable structure; the anterior end of the notch has moved far forward, and the reflected lamina has become a long narrow process extending downward and backward from its origin, largely under the shelter of the angle of the dentary. The bone is thin, perhaps some 2 mm. thick in a process 3 cm. in length and some 7 or 8 mm. wide, and its outer surface is essentially flat.

This process seems to be always present in cynodonts and must have served some function. R. W. Palmer in 1913 showed that this process of the cynodont jaw is extremely like the lower limb of the tym-

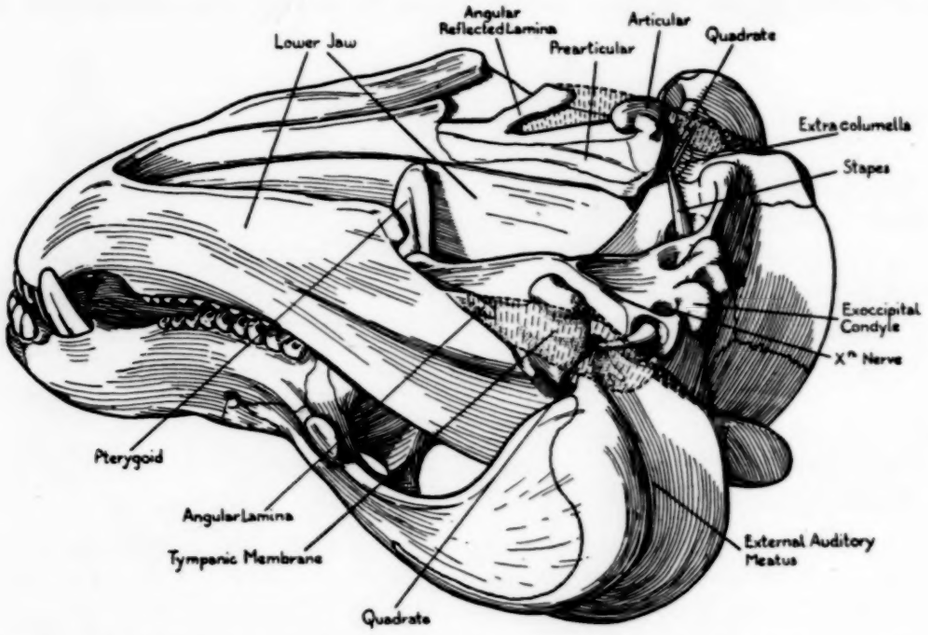


FIG. 7. Skull and articulated lower jaw of *Gomphognathus*, lying on the dorsal surface and seen obliquely from below. To show a possible position for a tympanic membrane and its extension to the reflected lamina. "Extracolumella" is the new process to the tympanic membrane discovered by Parrington (after Watson, 1951, reproduced with permission of Yale University Press).

panic bone of an "embryo" (pouch-young) marsupial and suggested that it supported a tympanic membrane.

The tympanic membrane: We have already seen that there is evidence of the existence in cynodonts of a tympanic membrane, a new formation, stretched across the inner end of the external auditory meatus at the level of the squamosal ridge at the end of the paroccipital process, connected by a newly formed outgrowth with the end of the stapes.

This membrane (fig. 7 [2]) may well have lain in a plane which would touch the outer surface of the large process, which exists in some specimens of *Gomphognathus* for attachment of the posterior pterygoid muscle to the articular, and continue to include the outer surface of the reflected lamina. Such a plane might well have been on a thin sheet of tissue, not necessarily of the structure of a tympanic membrane, which separated an air-filled extension of the tympanic cavity from the outer air.

Gregory (1910) pointed out that it was possible that the lower surface of the hinder part of the lower jaw of a cynodont had already come to be surrounded by the upper part of a tympanic cavity which had grown forward from the lower part of the hyoidean cleft, as the tympanic cavity of mammals always does during their ontogenetic development.

If there were a membrane supported as I have suggested in *Gomphognathus,* it could have played little part in the transmission of sound waves to the ear, but the anterior extension of the tympanic cavity, which its presence would imply, could act as a resonator in a way that is abundantly paralleled in mammals.

The cynodont condition is remarkable in the fact that though the hinder end of the dentary approaches to within 2 or 3 mms. of the squamosal, it never in any known specimen touches it, thus forming a double but coaxial articulation which is a necessary intermediate stage in mammalian evolution. In cynodont allies it produces no mechanical difficulties but lack of knowledge of it led even Gaupp into all kinds of absurdities, as "das Streptostylie-Problem."

It is evident that were the dentary of a cynodont descendent to touch the squamosal, the mechanical superiority of the new joint so formed would rapidly lead to its development, and that the hinder part of the jaw, the quadrate and stapes (probably already acting as a sound transmitting apparatus by bone conduction) would continue to function in this capacity. Freed from all heavy muscle stresses, however, they would be reduced in size and vibrations of the membrane stretched across the angular might well come to play a larger part in their movements. Under these circumstances any attachment of the angular bone to the skull might be expected to increase still further the importance of the tympanic membrane movement relative to those conducted through bones of the head and lead directly to the mammalian condition.

The musculus tensor tympani which controls the tension of the membrane is the old reptilian posterior pterygoid muscle, and the process to which this muscle is attached becomes the manubrium of the malleus.

Summary

The history of the sound transmitting apparatus of the mammalian ear is complex. It begins in an amphibian (labyrinthodont) ancestor with a tympanic cavity derived from the hyoid cleft communicating widely with the pharynx and extending upward and outward to end in a tympanic membrane (see Westoll, 1943). The membrane is stretched across a notch in the bony cranial roof, high up and relatively far forward. It is connected by a stapes with a fenestra ovalis placed ventrally on the side wall of the otic capsule.

The stapes is a complex bone, with its proximal end a footplate in the fenestra ovalis and its distal end in the tympanic

[2] From Watson 1951.

membrane. It has a ventral hyoid extension from the middle of its shaft, and proximally a process (the dorsal process) which articulates with the border of the fenestra ovalis and serves to control the motion of the stapes so that that bone may transmit vibrations of a tympanic membrane to a membrane closing the fenestra ovalis, which lies nearly at right angles to it.

The captorhinomorph ancestors of the mammal-like reptiles so altered the shape of their skull that the originally very small occipital surface was enlarged by the turning downward of the paroccipital process, and the quadrate gained increased support by the obliteration of the otic notch, so that its upper end could be directly supported by the paroccipital, and its lower end was strutted up by a huge stapes extending outward from the fenestra ovalis. The tympanic membrane thus disappeared, though the cavity remained. The stapes is still representative of all parts of its amphibian ancestor, the dorsal process being enlarged and moved laterally.

The next stage is one in which the skull becomes deepened to house the long masticatory muscles necessary to allow a very long mouth to open sufficiently, and in which the hinder part of the lower jaw becomes narrow but very deep in order to give girder strength to the jaw. As a result, the posterior part of the lower border of the angular around which the important anterior pterygoid muscle wraps on its way to its insertion, becomes cut off by a notch from the more anterior part of the lower border of the bone, which is carried backward as a "reflected lamina" to lengthen the insertion of intermandibular muscles.

The stapes at this stage is a large bone, its outer end (that which was formerly attached to the tympanic membrane) being directed into a "stapedial recess" in the hinder and inner surface of the quadrate and pterygoid, to which bones it is attached.

The next stage is one in which the ventral migration of the outer ends of the paroccipital processes is carried much farther so that they support the quadrates nearly to their lower ends.

During this episode the temporal fossa, introduced to allow the belly of the jaw muscles to thicken during their shortening, eats into the flat cranial roof from which these muscles arose, and in consequence their origin migrated onto the upper and hinder borders of the fossa. This origin allows the muscles to increase in cross sectional area and leads to a bowing outward of the zygomatic arch. The posterior surface of the squamosal is in contact with a depressor mandibuli muscle which is inserted into a retroarticular process so that by contraction it can open the mouth. Later this muscle vanishes and some new arrangement arises to open the mouth, and the flange which bounds the area of insertion of the neck muscles and originally lay in contact with it remains. The stapes ends in a large stapedial recess, there being no tympanic membrane.

In the next succeeding stage some influence, whose nature is unknown to me, leads to a general reduction of the height of the skull. The chief part of this reduction falls on those structures which lie below the level of the base of the brain behind the transverse flanges of the pterygoids.

This reduction of height is so considerable that vertical temporal muscles would necessarily be too short to allow the mouth to open to a reasonable amount. Thus the muscles tend to lie horizontally, their origins being or a back-turned border of the squamosal behind the temporal fossa, and their insertion on a new outgrowth of the dentary which rises above the upper border of the surangular.

The hinder part of the lower jaw is thus relieved of all large bending stresses and serves merely to transmit longitudinal forces to the front face of the quadrate.

The quadrate, which lies in a depression on the front face of the squamosal immediately lateral to the paroccipital, thus becomes of small vertical height though its articular surface retains its original

width. It retains for some time its original support by a special ramus of the pterygoid and retains or develops a contact with a quadrate ramus of the epipterygoid lying above it. The end of the stapes, still completely homologous with that of a labyrinthodont, lies in a stapedial recess in the quadrate and pterygoid, held down on its floor by a distally placed dorsal process.

The next event of importance is that the still surviving tympanic cavity comes nearly into contact with the skin at a point where the hinder surfaces of the squamosal and tabular bones form a ridge bounding the occiput at the end of the paroccipital process. This point of contact becomes a tympanic membrane and a new process, partly of bone, grows out from the stapes to reach it behind a new firm contact it gains with the quadrate. At this stage the stapedial recess vanishes.

Meanwhile the lower border of the hinder end of the dentary has grown downward below the angular as a muscle insertion, and the hinder part of the jaw becomes very slender, the notch and reflected lamina moving forward largely mesial to the angle of the dentary.

It seems that at this stage a further extension of the outgrowth of the hyoid cleft which is the tympanic cavity had surrounded the lower surface of the hinder part of the lower jaw and that there was a continuous outer surface of skin from the much reduced reflected lamina to the new tympanic membrane, the inner surface of this layer being in some individuals in contact with a process (that to which the posterior pterygoid muscle was attached) of the articular.

At this stage the animal heard by conduction from the tympanic membrane through the stapes, and also by bone conduction.

During these changes and inseparably tied up with them is a further continuance of the reduction in height of the quadrate, and the disappearance first of the quadrate ramus of the pterygoid and then of the quadrate ramus of the epipterygoid. When this has happened the quadrate is held in place in a depression in the anterior face of the squamosal, which has a rounded concave roof and a flat vertical back, by the pressures it transmits from the muscles attached to the dentary, and the tissues which lie between the two bones.

At this stage a special external auditory meatus analogous in position and presumably in nature with the cartilaginous tube of platypus comes into existence.

In the most advanced mammal-like reptiles, the tritylodonts, some of which are contemporary with actual mammals, the nature of the wear on the teeth shows that the jaw slid back and forth, and that the movable joint must have been between the quadrate and the squamosal. In fact, in *Bienotherium* and, as Dr. Kühne has shown me, also in *Oligokyphus,* the quadrate is free to move, in effect articulating with the hollow summit of its old recess in the squamosal, the vertical sheet of squamosal which had earlier supported it having vanished.

Once this condition has been reached it is very easy to see that a further back growth by two or three milimetres in a skull 120 mm. long would bring the hinder end of the dentary into a contact with the squamosal, co-axial with the old quadrate-articular joint. All that is necessary is to enlarge this new joint, whose mechanical superiority is obvious, and to retain the existing stapes, quadrate, articular and angular as the mammalian stapes, incus, malleus and tympanic with a reduction in size made possible by their supercession so far as concerns their old function by another arrangement and a general desirability of a lower weight of the sound transmitting elements. And the amount of the size reduction may have been quite small, for *Oligokyphus* with a skull about 90 mm. long has a quadrate only some four millimetres high and wide.

Thus the characteristic arrangement of the sound-transmitting apparatus of the mammalian ear arose as an unforseeable

result of many changes in the head structure of mammalian ancestors, which in part seem to have depended on some mechanism which led to a reduction in depth of all structures which lay below the base of the brain, but all of which represent reorganizations which improved the mechanical efficiency of the jaws, and indeed of the animal in general. They differ in no respects from changes which can readily be explained by natural selection, and in the end they happen to leave the animal with what is essentially a mammalian ear, capable no doubt of much further refinement.

The animals which are dealt with in this story are not in fact actually members of a single line of descent leading up to mammals. For example, the final form, a trity-lodont, cannot have been ancestral to any known group of mammals with the possible exception of the Monotremata. Nor was it in fact a descendent of *Protacmon*. The Cisticephalus zone gorgonopsids are not in fact derived from the therocephalian *Lycaedops,* and so for all the animals referred to.

None the less, our now very extensive knowledge of these reptiles makes it evident that the phenomenon of parallel evolution is so widely displayed among them that so long as we pick the members of our series from not too remote groups, and of the *right time,* we shall not be seriously in error. And if we can use, as in fact we usually can do, the same series of animals for the investigation of the structural changes in a large number of parts of the body we gain further assurance that we are justified in our procedure.

Thus it is in every way likely that the story of the evolution of the mammalian sound-conducting apparatus of the ear as seen in an actual series of ancestors, although it would be immensely more detailed, would not in general character differ much from that I have set out above. The series of forms I use covers an actual period from the beginning of Permian times to a point low in the Jurassic, about sixty million years, perhaps fifteen to twenty million generations. But the amphibian ancestors of the pelycosaurs lay still further back.

During this immense period, as long as the whole Tertiary in which the deployment of mammals took place, change is constantly going on, and going on in such a way that the mechanical efficiency of the animals is steadily increased. Their limbs change so that locomotion becomes more rapid and precise. Their rib cage alters so that mammal-like breathing is achieved, and so on for any process whose development is studied. All these changes, although they usually proceed in definite directions common to many groups, are of such a kind that they can be accounted for by "natural selection." But the changes in the lower jaw, quadrate, squamosal and stapes which ultimately lead to the mammalian ear ossicles, are going on continuously throughout this immense period of time. In their individual natures they do not differ at all from those which can be seen in other parts of the skeleton. Indeed to a great extent they are changes which improve the mechanical efficiency of the bite, or of the attachment of the head to the neck. They are equally susceptible to a "natural selection" explanation. Only those changes in pterygoid, epipterygoid, and quadrate which seem to be related to a widespread reduction of the height of all structures which lie below the base of the brain, may perhaps depend on some different and unknown mechanism.

But the complete change of function from jaw articulation to hearing which occurs during this evolutionary process is exactly the kind of matter which has been held to demand a special "Macro-evolution" mechanism, distinct from and of a different nature to "natural selection." Those who believe in the existence of such macro-evolution, appear to hold that it is brought about suddenly perhaps by a single change in the genetic mechanism, that at a single jump calls into being a new major group, or a structure or organ for which it is difficult to conceive the inter-

mediary stages by which it could have been derived from an earlier structure.

The sound-conducting mechanism of the mammalian ear is such a structure. The struggles of embryologists to invent a method of conversion of a lizard skull, with its movable quadrate, into that of a mammal, show that it is not easy to conceive the transformation without knowledge of the actual intermediate conditions. Indeed the mammalian ear is a typical event of the kind attributed to macro-evolution. But the story set out above shows that the change is brought about, without any reference to hearing for the greater part of the process, to improve the jaw apparatus and to get rid of a skull inconveniently deep. An essential part lies in the details of structure of the large sphenacodont pelycosaurs. Another seems to have lain in a need to strut up a long quadrate by an enormous stapes. And the character of this stapes has its origin in geometrical considerations of the labyrinthodont skull. Thus, there is no reason at all to postulate any unusual mechanism for the evolution of the mammalian sound-transmitting apparatus. The changes which lead to its formation occur over a period of many millions of years and generations, owe their nature to ordinary mechanical needs having nothing to do with hearing, and in one case are part and parcel of a set of widespread changes whose determination is obscure, but which proceed slowly.

Thus, there is no sign of any special process of macro-evolution in this typical case. All the other cases which have been adduced are incapable of investigation historically, and they are outside the field of palaeontological enquiry, the only way in which we could obtain direct evidence of their nature.

Literature Cited

Broom, R. 1936. On the structure of the skull in . . . Therocephalia. Phil. Trans. Roy. Soc. London, (B), **226**: 1–42.

——. 1948. A contribution to our knowledge of the vertebrates of the Karroo. Trans. Roy. Soc. Edinburgh, **61**: 577–629.

Efremov, J. A. 1940. *Ulemosaurus svijagensis* Riab. Nova Acta Leopoldina, N. F., **9**: 155–205.

Gaupp, E. 1913. Die Reichertsche Theorie. Archiv f. Anatomie u. Physiologie, 1912. Anat. Abt., Supplement-Band.

Goodrich, E. S. 1930. Studies on the structure and development of vertebrates. Macmillan. London.

Gregory, W. K. 1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., **27**: 1–524.

Gregory, W. K., and Adams, L. A. 1915. The temporal fossae of vertebrates in relation to the jaw muscles. Science (n.s.), *XLI*, 763–765.

Olson, E. C. 1944. Origin of mammals. Geol. Soc. America Special Paper 55.

Palmer, R. W. 1913. Note on the lower jaw and ear ossicles of a foetal *Perameles*. Anat. Anz., **43**: 510–515.

Parrington, F. R. 1946a. On the cranial anatomy of cynodonts. Proc. Zool. Soc. London, **116**: 181–197.

——. 1946b. On the quadratojugal bone of synapsid reptiles. Ann. Mag. Nat. Hist., ser. 11, **13**: 780–786.

——. 1948. Labyrinthodonts from South Africa. Proc. Zool. Soc. London, **118**: 426–445.

——. 1949. Remarks on a theory of the evolution of the tetrapod middle ear. Jour. Laryngology and Otology, **63**: 580–595.

Price, L. I. 1935. Notes on the brain case of *Captorhinus*. Boston Soc. Nat. Hist. Proc., **40**: 377–386.

Romer, A. S., and Price, L. I. 1940. Review of the Pelycosauria. Geol. Soc. America Special Paper 28.

Sushkin, P. P. 1927. On the modifications of the mandibular and hyoid arches and their relation to the brain-case in the early Tetrapoda. Palaeont. Zeitschr., **8**: Heft 4, 263–321.

Watson, D. M. S. 1912. On some reptilian lower jaws. Ann. Mag. Nat. Hist., ser. 8, **10**: 573–587.

——. 1914. Notes on some carnivorous therapsids. Proc. Zool. Soc. London, **69**: 1021–1038.

——. 1921. The basis of classification of the Theriodontia. Proc. Zool. Soc. London, 35–98.

——. 1926. The evolution and origin of the Amphibia. Phil. Trans. Roy. Soc. London, (B), **214**: 189–257.

——. 1948. *Dicynodon* and its allies. Proc. Zool. Soc. London, **118**: 823–877.

——. 1951. Paleontology and modern biology. Yale Univ. Press.

Westoll, T. S. 1943. The hyomandibular of *Eusthenopteron* and the tetrapod middle ear. Proc. Roy. Soc. London, (B), **131**: 393–414.

NOTES AND COMMENTS

THE CHRONOFAUNA AND QUANTUM EVOLUTION

JAMES R. BEERBOWER

University of Chicago, Chicago, Illinois

Paleontologists have long recognized that periods of rapid evolution, *i.e.*, the quantum evolution of Simpson, are associated in some degree with changes of the physical environment. This association, however, is seldom precise nor do regular pulses, temporally related to diastrophic events, appear to have the reality suggested by some enthusiasts (see Journal of Paleontology, vol. 26, pp. 297–394, 1952). Olson (1952) has analysed certain of the relationships between evolution and changes of environment with particular reference to the interaction of the faunal elements, and he suggests that rapid evolution is most likely during the breakdown of the chronofauna. This chronofauna, or rather the evolving ecosystems of which a given chronofauna is partial expression, must have achieved a relative balance of structure during its period of development. In addition, the factors acting within it and on it must have approached equilibrium. With an alteration of the physical environment some ecologic thresholds of the ecosystem or of certain of its components may be crossed and the system disrupted. With this disruption the balance is destroyed, and the environmental relationships will assume a radically different configuration, one in which some few factors are likely to be much more important than the remainder. As a consequence selective pressures will be greatly altered in direction and magnitude. Under these conditions large mutations, in general deleterious but providing response to one of the small number of important selective agents, are much more likely to be incorporated into the population. Further, the unusual environmental stresses are likely to reduce population size of most of the concerned species and to limit distribution to scattered favorable areas. The most extreme action will reduce the species populations to small isolated units in which genetic drift, *i.e.*, the Sewell Wright effect, would be of importance. Lesser action would break the population into small, partially isolated units favorable to rapid evolution. Systemic mutations (disregarding the genetic basis of such mutations) might well spread very rapidly and alter the character of the species in a very few generations. Such mutants might be considered as arising *de novo* during the period of environmental stress or, more probably, as being present at a very low frequency prior to this period. That such a process is an initial step in the formation of higher categories appears to be a distinct possibility. However, the positive demonstration of this process by a study of fossil material seems unlikely although it may be indicated by negative evidence.

The ideas suggested here bear a similarity to parts of the macroevolutionary theory of Goldschmidt and others, but there are important differences. First, higher categories probably arise in several ways, and second, the origin of these categories is not different in kind but rather in magnitudes of rates from that of lower categories. A strong dichotomy in rates is possible if the ecosystem has reality, for either the system stands and evolves, rather slowly, as a unit or it breaks down and its surviving elements evolve rapidly toward a new system. The processes, however, are the same in either case. A third difference from Goldschmidt's theory is that the higher category does not arise at this single mutational step but, on the contrary, the adoption of the mutation initiates an evolutionary trend that leads to a major radiation. This radiation then, based on a common ground plan of characters extending far beyond those involved in the original mutation, is the higher category. The difference on this point would seem to be one of differing concepts of the nature of higher categories and of little scientific importance.

The hypothesis offered here is entirely theoretical and no paleontologic proof can be adduced inasmuch as the interpretation of fossil assemblages depends upon use of the theory, but it can be said that some of the evidence conforms with the idea. The correctness of the whole evolving ecosystem concept can only be adjudged by the review of data gathered by the geneticist and ecologist and by a detailed mathematical analysis of the properties of this system.

REFERENCE

OLSON, E. C. 1952. The evolution of a Permian vertebrate chronofauna. Evolution, vol. 6, pp. 181–196.

COMMENT ON "HOW MANY SPECIES?"

GEORGE C. STEYSKAL
Grosse Ile, Michigan

The "reasonable guess" by G. G. Simpson (Evolution, Vol. VI, No. 3, P. 342) concerning the number of species that have occurred in the whole history of life seems open to serious doubts as to its reasonableness. The matter hardly seems as simple as Simpson has outlined it. His formula *ac/b* would seem to indicate either that he believes that life started with a batch of new creations of roughly the same number as contemporaneous species or that an immense number of species have become extinct, or in other words that enough phyletic lines have died without giving rise to new forms to result in an "all-time average, which might be guessed as somewhere between 250,000 and 1,000,000" as compared with a contemporaneous total of 2,000,000 ("a reasonable estimate, perhaps on the conservative side").

If we subscribe to the theory of the monophyletic origin of life, or at most to a narrowly oligophyletic theory, with the number of species increasing in a kind of geometric progression tempered by extinction, the all-time average in my opinion must be much lower than Simpson's guess. Since so little is known about durations of species, rate of production of new forms, etc., in past geological periods, a reasonable guess is still out of the question.

CAVE FISH EVOLUTION

CHARLES M. BREDER, JR.
American Museum of Natural History, New York, New York

There has recently appeared a most interesting and provocative study [1] on the African cavefish, *Caecobarbus geertsii* Boulenger, which differs from the genus *Barbus* only in depigmentation and loss of integrity of the eye. The work is confined almost entirely to morphological allometry through which interpretations are extended into probable physiological activities. The acceleration or deceleration of growth, as registered by the relative size of organs or parts, can, of course, be considered a naturally produced "graph" of the history of the metabolism of the organism. The author by applying such considerations has attempted to interpret the effects of cavern environments by relating these growth changes to the known conditions in the caves studied.

Quite properly he has emphasized the point that a cave environment is a complex of ecological influences and should not be considered merely the equivalent of the outside environment with the light eliminated. Moreover, in so doing, it would seem that the importance of light as an environmental factor has been de-emphasized beyond warrant. By minimizing this ecological element the author has arrived at an explanation of the causes of eye degeneration and depigmentation in which he relates these effects directly to reduced food intake and to lowered metabolic rate. Since the eyes of fishes are organized early in development and grow rapidly at first and because the cavefish subsisted on a restricted food supply and therefore had a reduced metabolism, the author reasons as follows. "Indeed, according to the hypothesis, the growth of the eye should be particularly liable to changes in body growth velocities and *its disappearance would be the logical consequence of the retardation of body growth.*" [2] It can be shown that a lowered metabolic rate, such as that induced by a lower temperature, promotes the development of somewhat smaller eyes in certain fishes than when they are reared in higher temperatures. However, this fact simply cannot be extrapolated to account for the lack of development or subsequent involution of the eyes of fishes on a reduced food intake. Such changes in eye size do not suggest the dissolution of the organ nor its accompanying loss of function.

The loss of pigment is accounted for in the following similar fashion. "The formation of pigment seems to be closely parallel to the growth particularities of the eye. Melanine pigment is usually laid down within a short period in early life, without further increase, at least in most fishes. We can, therefore, consider it as a steeply allometric process, whose dependency on growth rate accelerations is even stronger than eye growth." Actually melano-

[1] Heuts, M. J. 1951. Ecology, variation and adaptation of the blind African cavefish *Caecobarbus geertsii* Blgr., Ann. Soc. Roy. Zool. Belg., **LXXXII**: 155–230.

[2] Italics his.

phores form early in the embryonic life of teleosts and go on as a highly dynamic process throughout the life of the individuals. The phrase "without further increase" is extremely misleading for it is no more true of melanophores than it is of—say, lymphocytes. Both go on forming and being destroyed for the life of the animal and in both cases the numbers of cells present vary widely as they are called into being for current needs. Great quantities of lymphocytes are produced to stem infection while in many fishes the simple process of looking at a dark background will induce the copious production of melanophores—only, however, in the presence of light.

Although the mechanism responsible for the depigmentation and destruction of eyes in cave animals is far from being fully worked out, it would seem to be premature to attempt to refer such loss to an inadequate food supply. The fact remains that the very things lost are those most importantly and directly operating in reference to light: vision and the appearance of the animal in reference to pattern and hue. The presence of vision and light and what is seen (background) play controlling roles not only in the movement of the melanin granules but also in the increase or reduction of the number of melanophores present. Therefore, it is difficult to refer their loss in the absence of light to food restriction, especially since there are no other unequivocal evidences of inadequate food. In illuminated environments, an inadequate food supply usually leads to a stunted or dwarfed population which otherwise is normal. This common result of not a sufficiency of food is a matter well known to pond culturists.

It was impossible to read this document without being constantly reminded of the many striking similarities and equally striking differences between this fish and the Mexican cave fish, *Anoptichthys jordani* Hubbs and Innes, which we have had under study for some years. Perhaps even more striking are the differences in interpretation between the two studies. The fishes are of such similar appearance that at a little distance it is impossible to distinguish them. Although both are ostariophysian fishes one is a cyprinid and the other a characin. That they are so similar in appearance should not be too surprising since the genus *Barbus* and *Astyanax* show frequent parallelisms in numerous species not associated with caves. One of the marked differences would seem to be that the characin is a very hardy fish and breeds readily in captivity whereas, so far at least, the cyprinid has not been bred in captivity. Like the situation in Africa, the Mexican caves which are inhabited are confined to what is evidently one underground water-way in a region honeycombed with other caves which are barren of fishes. There is a wide seasonal fluctuation in both sets of caves, but unlike the African caves, all Mexican caves containing characins were well ventilated. On the assumption that the marks on the scales of *Caecobarbus* are annuli, Dr. Heuts indicated a very slow growth for the species, which condition he referred to a small food intake. Earlier studies on the characins indicated an ordinary growth rate on a similar assumption. In aquaria, these fish thrive and show growth rates typical of such small fishes. In the characin a graded series from the pigmented and large-eyed river fish to the fully depigmented and blind cave fish of several population varieties have been found. In the cyprinid, the various populations show variations evidently of a similar sort, but there are no intermediates with any of the numerous surface living *Barbus* and it is not clear from which, if any, of the surface species present *Caecobarbus* was derived. The characin definitely breeds in the dry season, at least, whereas the cyprinid was not found in breeding condition then, in fact young fish were found in only one of six populations. A very good case is made out for the small food supply available to *Caecobarbus*. Such is not the case with *Anoptichthys* and there is no reason to believe that there ever was. Caves which are not populated with bats are full of debris from the outside world which comes in by way of the various sink holes and other openings. Insects are abundant. Caves with bats have an even richer food supply. The stomachs of the fishes were found to be well packed with the remains of insects, often gotten by way of bat droppings on which these fish gorge themselves. As this system of caves runs down a valley in which the drainage is now all underground, there is no reason to suppose, as this geological process progressed, that the fishes ever had less than the present food supply. Thus, in addition to the reason given previously, and whatever may be the case with the African caves, *practically identical depigmentation and eye loss has evidently here proceeded in the presence of abundant food.*

The growth curves given for the six cyprinid populations are most extraordinary. Five of them may reflect erratic starvation, but one of them, which Heuts calls "the most simple one," when plotted as an *arithemetic* graph, is best approximated by a straight line, indicating that for some eight years this population showed no diminuition of growth at all! When a similar examination was made of the Mexican cavefish, it was recognized that these marks were not necessarily annual nor even based on regularly recurring events. They did happen to indicate on that basis, however, what would not have been an unreasonable growth, slowing with advancing years. It might be that in the African cavefish the marks studied by Heuts are produced by some more or less erratic environmental factor or several of them. In such a case

the marks alone, especially when not definitely connected with their ecological cause, could be completely misleading. It is worth noting that of the twenty known genera of blind and depigmented cavefish, eight are from the southern United States and northern Mexico, three each from South America, none from Europe and the remaining six from four widely scattered islands. Evidently, this American area is markedly favorable to the process. It would seem improbable, without extensive evidence to the contrary, that any one hypothesis could cover the relationships of all cave fish to their caves. It would seem, a priori, that more probably each one traveled a slightly different route.

Much is made of the "fitting" of these cave populations of *Caecobarbus* to their caves. The characins discussed above thrive under a great variety of water and food conditions in aquaria and fish ponds in the light. By now some thirty generations have been reared in a bright Florida greenhouse and it would seem that their blindness alone stands in their way of successful surface life. Knowledge of this difference has led Dr. Heuts to infer that his African fish are better integrated with their cave environment than are the Mexican fishes with theirs. Considering the considerable lack of young fishes encountered in the African caves and the peculiar growth features, it could be equally as well thought that the African caves present today, at least, a much less friendly environment for fishes than do the Mexican caves. This could well involve more than food restriction, for the author indicates the presence of excessive amounts of carbon dioxide.

REVIEW OF PRINCIPLES OF ORGANIC EVOLUTION[1]

GLENN L. JEPSEN
Princeton University, Princeton, N. J.

Lindsey first published many sections of this book, so curiously anachronistic and inaccurate in spots, in 1929, in his "Textbook of Evolution and Genetics." He attempted then to evaluate the bearing of genetics, during the development of the subject in the first quarter of the twentieth century, upon the larger problems of evolutionary processes and to rationalize the deficiencies in some of the theories of evolution which were then current.

At that time he saw in Lamarckism "the only explanation of *how* change occurs in organisms" but no explanation of progressive change in species, and in Darwinian selection he found a useful theory of adaptation but no explanation of the origin or occurrence of variations. Consequently he decided that all the existing theories of evolution were "of little individual value as nuclei for an explanation of the processes of evolution." Throughout the volume, however, he expressed the hope that Lamarckism would in the future receive increased attention and support because he sensed "a marked tendency among scientists to feel that Lamarck's views have more to commend them than has been admitted" and because "the idea persists that acquired characters contribute to the heritage."

Now, after the century's second quarter it is interesting to compare Lindsey's conclusions of 1929 with those of 1952. During this time the data and methods of genetics and paleontology have been extensively advanced and developed, and various theories of evolution have been tested and modified. Unfortunately, Lindsey seems unaware of much of the recent work in these fields. The new book assumes an elementary knowledge of genetics and hence omits a long section on primary genetics which appeared in the earlier volume, but many parts including some on paleontology which were out of date even in 1929 are reprinted without change.

He knows that Lamarckism has now been virtually abandoned, in most of the world, as a field for fruitful investigation, but he is not convinced that the numerous experiments which have been devised to test the inheritance of acquired characters have been either inconclusive or clearly contrary to the facts of life. He remarks that there is such a general acceptance "of the idea that natural selection and mutation are the only valid processes of evolution" that anyone who questions their adequacy and "brings up the problem of individual adaptability still runs the risk of being condemned as a neo-Lamarckian." However, this risk is "willingly assumed" by him because "Until we have arrived at a final solution of evolutionary processes, no approach can be dismissed as unprofitable," and because "the consideration of Lamarck's theory of evolution by modern biologists has resulted in a predominately critical attitude involving a measure of ridicule which is not complimentary to the critics." It would be well, he thinks, to abandon the "traditional antagonism" between the Lamarckian and Darwinian schools and to seek a "dispassionate con-

[1] Principles of Organic Evolution by Arthur W. Lindsey. C. V. Mosby Co., St. Louis, Missouri, 1952: 1–375, figs. 1–216. $5.75.

junction" of their values, inasmuch as "the basic separation of the original theories . . . is based on a misconception." As an explanation of this misconception he says that "The essential difference between acquired characters and the hereditary variations emphasized by Darwin . . . is therefore not a matter of fundamental heritability, but only of the conditions leading to their phenotypic expression."

He regards mutation and selection as inadequate to explain evolution because "Evolution has apparently not been haphazard, but directly adaptive at every step, and the idea that it may result from a foundation of haphazard genetic changes or random mutations with assumed preadaptive value seems scarcely logical . . . In short, evolution as we see it in the records of the past has apparently proceeded in spite of much mutation and under the added burden of eliminating the many unfortunate mutant individuals." This leads him to observe that "How mutations come about and their possible association with individual reaction to the environment are too important problems to be evaded longer," and that "The fact that adaptive reactions are not known to cause mutations does not preclude that possibility, and the progressive ancestral sequences of the past strongly suggest it." This theme is repeated in different words many times, and he predicts that the probable future explanation of the process of evolution lies in the accumulated knowledge of biochemistry where "there is abundant evidence . . . for the correlation of individual adaptability with the mutation theory."

It is not easy to follow Lindsey through his descriptions and interpretations of facts and his reasoning, for, although his writing is sometimes interesting and ingenuous, the whole work appears to have been assembled piecemeal and never properly integrated. Repetitious references to some topics, each time with slight changes of emphasis and meaning, give the reader a frustrated sense of not quite knowing what the author is driving at or why he is doing so. In view of the title and the potential use of the book by students it is reasonable to inquire why he has assembled such a series of observations and opinions about biology and paleontology. Perhaps the explanation may be found near the end of the book in his comments about society, learning, and man's future, and particularly in the statement that "If we could know that individual response to environmental conditions is an important factor in organic evolution, the implication for our educational procedures would be tremendous. We have considered the possibility and found it good." He holds a devout hope that somatic and even mental responses in the individual might cause adaptive mutations, that there is a "possibility of hereditary modification through individual behavior," because the germ plasm may be "responsive, like somatic tissues, to the conditions surrounding it."

There is little doubt that the author is sincerely interested in finding and teaching the truth, that his desire to believe in Lamarckism is in line with his comment in the Preface that he wants to consider "the most recent contributions of Lamarckian flavor . . . impartially with those of genetics." Some of the experiments and observations he cites as support for Lamarckian notions, however, have been quite differently interpreted by other authors.

He apparently ignores or is unaware of the fact that most of the recent work of Lamarckian flavor has developed in Russia. Nowhere in the book have I found a reference to Lysenko or to other recent Soviet geneticists. In the list of nine references at the end of Chapter 16 on "Lamarckian Theory" the most recent work was published in 1939, and the other dates range from 1809 (Lamarck) to 1913. (Incidentally, this chapter opens with the incredible statement that "Historically the forerunners of Lamarck offered nothing that has left its imprint on the evolutionary thought of today.")

It is important to observe, in justice to Lindsey, that his present conclusions are a continuation of his long search for justification of his wish to believe in Lamarckism, and not the result of recent influence by official Soviet attitudes toward the data and meaning of genetics. Otherwise his statements might be distorted and misused as propaganda favoring or supporting the utterances of Lysenko and his associates. To this date, it has been impossible for Lindsey or anyone else on this side of the Iron Curtain to submit many of the recent assertions of Russian geneticists to the impartial and nonpolitical tests of free science, or even to know fully what these claims are, and there is no immediate prospect of a greater penetration of the various social, political, and linguistic barriers. Lindsey's knowledge, however, about the idea of the inheritance of acquired characters, the tests which have been put to it, the reasons for its present infamy, and its position in Russian science could have been greatly extended by reading various works by Zirkle and other modern authorities, none of whom are mentioned in the book.

Like many other evolutionists Lindsey regrets that the promise which genetics seemed to make twenty five years ago, and still holds in less degree, for the solution of many fundamental problems of phylogenetic processes has not come to full fruit. He is unorthodox but not alone in lamenting the fact that, although genetics has become a highly sophisticated group of sciences, many gaps between genetics and morphogenesis are still unbridged, and that some of the promised answers must lie in other fields which are yet unexplored. He hopes that increasing pres-

sures for the reconsideration of the anomalous and discarded data of formalized genetics will cause a reconstruction of the ideas derived from the subject.

Following an introductory chapter and one on The History of Evolution the remaining nineteen chapters in the book are placed in five groups—(1) Relationship of Organisms, (2) Evidences of Evolution, (3) The Evolution of Existing Forms, (4) The Process of Evolution, and (5) The Importance of Evolution in Human Life.

Errors of fact and inference and emphasis occur throughout the book. Many are easy to sense but hard to correct without lengthy explanations. Students will be confused if not actually misled by such phrases and statements as the following. "The chromosomes of the salivary glands of the giant race of *Drosophila* were much larger than any others." ". . . in the horse . . . the first molar is vestigial or lacking." "We have mammals which resemble fishes . . . and . . . other cases of mimicry." (Later, it is explained that the term convergence is usually used rather than mimicry for this phenomenon.) ". . . in contrast with the conical form of all teeth in the reptiles." "In the Cambrian and Precambrian, however, earliest periods of the Paleozoic. . . ." "One flying mammal, *Galeopithecus*, the 'flying lemur.' . . ." In *Mesohippus* "The eye . . . orbit was closed behind. . . ."

Most of the figures and the text references to them give no information about the sizes of the objects represented. In the sections on paleontology some of the phylogenetic diagrams are archaic and others are confused, inconsistent, and mistaken. It is most unfortunate that recent authors were not consulted before these errors got into print.

A reviewer finds himself regretting that the enthusiastic author, obviously trying to do a good teaching job and pleading earnestly for increased learning, has not used more modern sources for his observations and conclusions. Everyone will agree with his comments that our knowledge is meagre and that investigations of the processes of evolution have by no means reached the limits of possibility.

REVIEW OF INVERTEBRATE FOSSILS[1] AND PRINCIPLES OF INVERTEBRATE PALEONTOLOGY[2]

NORMAN D. NEWELL

New York, New York

The teaching of introductory courses in invertebrate paleontology involves certain difficulties which in large measure stem from traditional attitudes toward the subject. Historically, this subject has been the "handmaiden" of geology with conscious emphasis on the utilitarian aspects of fossil invertebrates, *i.e.*, their exceptional value in recognition and dating of stratigraphic units, and considerably less attention has been given to the animals of which these are the remains.

This attitude has tended to result in a disproportionate emphasis on familiarity with a large number of guide fossils. To some teachers, indeed, this sort of knowledge is the ultimate objective of training in invertebrate paleontology. In this case, the uninitiated geology student, usually quite innocent of any prior contact with formal zoology, is quite likely to be repelled by seemingly endless and irrelevant morphological and taxonomic details. The grand underlying principles of paleontology embodied in evolution, ecology and stratigraphy, which might provide the framework for a thoroughly fascinating and meaningful introduction to paleontology, are too often subordinated to the conventional morphologic-taxonomic treatment.

This mode of approach somewhat resembles that usually followed in elementary courses in mineralogy, but it is quite unlike the more general and philosophical treatment which commonly characterizes introductory course work in chemistry, physics, botany, and zoology. The latter mode is more attractive to most students and better provides a broad perspective of the subject.

Two new, thick, and handsome McGraw-Hill books on invertebrate fossils are important milestones in the development of invertebrate paleontology. To a certain extent they show some departure from the traditional systematic treatment, but there is still substantial emphasis on morphology. Although the two books differ from each other somewhat in mode of treatment, Invertebrate Fossils, by Moore, Lalicker, and Fischer, and Principles of Invertebrate Paleon-

[1] Invertebrate Fossils, by Raymond C. Moore, Cecil G. Lalicker and Alfred G. Fischer. 23 chpts. 766 pp. 455 figs. McGraw-Hill, New York, N. Y. (May 28, 1952). Price, $12.00.

[2] Principles of Invertebrate Paleontology, by Robert R. Shrock and William H. Twenhofel. 16 chpts. 816 pp. 470 figs. 24 tables. McGraw-Hill, New York, N. Y. (January 2, 1953). Price, $12.00.

tology by Shrock and Twenhofel, both are in many respects up to date and comprehensive books; they cover about the same material and they are priced the same, well above the usual level of elementary college textbooks. Many professional paleontologists and advanced students will find both books to be valuable reference works. Both contain a great deal of authoritative material not heretofore readily available to American students on all of the major groups of invertebrate fossils. The respective authors are sanguine, however, in their conviction that the new books are entirely suitable introductory textbooks for college students. The books are crowded with technical detail, and are expensive. Neither sufficiently emphasizes the broad principles and philosophy of the subject needed to orient the serious student and there is very little direct reference to the historical development of the subject.

Invertebrate Fossils is a wholly new and very laudable book. Two features are especially outstanding on even casual inspection, these are: (1) the many unusually effective illustrations, and (2) the modern treatment of many subjects. The book is illustrated by a large number of line drawings, most of which were made by the authors. Hundreds of these, even more than needed in a textbook, represent characteristic genera of fossil invertebrates. Other ingenious diagrams are designed to explain morphological details and to suggest environmental modes. A few of the text figures are a little too schematic and would be somewhat improved by reduction and regrouping (*e.g.*, figs. 2–10, 2–11, 2–12, 2–13), but for the most part the illustrations are excellent.

The introductory chapter is an all too brief, but very good, treatment of some fundamentals of paleontology. The authors call attention to the value (not *uses*) of fossils as (1) stratigraphic indicators, (2) as records of past forms of life showing the course of evolution and (3) as evidence of changing environments and geographic patterns during geological history. There is a concise review of the elements of zoological nomenclature, and description of taxonomic categories used in classification of animals. Adaptation to environment, ecologic factors, animal development, life histories, relative growth, evolution and extinction, all of these subjects, covered in the first chapter, are of fundamental importance and might well have been allotted much more space. Consideration of the biogenetic "law" (pp. 28, 30, 40, 557) is more or less conventional and the reader is likely to derive the impression, probably not intended, that recapitulation is really quite prevalent among invertebrates. The student might be impressed to learn that hypothetical phylogenies in certain groups (*e.g.*, the Foraminifera) are based partly on the assumption, often without adequate stratigraphic support, that ontogenies usually recapitulate phylogenies. Paedomorphism is defined (pp. 20, 491), but clear explanation is lacking that recapitulation and paedomorphism are only extreme cases in a whole spectrum of situations. A discussion of von Baer's "laws" of development would have been pertinent here. Useful diagrams based on numbers and ranges of genera show stratigraphic distributions of major groups objectively.

One of the many functions of textbooks is to acquaint students with prevalent usage and established practice. In Invertebrate Fossils a few new departures are made in classifications of coelenterates, brachiopods, pelecypods, cephalopods, arthropods and crinoids, and a new and simplified scheme of notation is introduced for hinge characters of pelecypods. Judgments vary, of course, but some may question the appropriateness of introducing innovations in classification and terminology in a work of this kind. As first fruits of the international Treatise of Invertebrate Paleontology are about to appear, it seems desirable for such revision to fall within the framework of the larger collaborative effort.

Principles of Invertebrate Paleontology is announced as a second edition and revision of Invertebrate Paleontology by Twenhofel and Shrock which since its appearance in 1935 has been the standard American textbook on the subject. The new book, while retaining the conservative mode of treatment of its predecessor, is greatly expanded and shows considerable improvement in text material and illustrations, especially the many half tone reproductions. Inclusion of several new chapters on groups rarely, or perhaps never, preserved as fossils (comb jellies, various phyla of worms, Phoronids, and so on), is helpful in pointing up the unevenness of the fossil record. Useful selected bibliographies are given at the end of each chapter.

It is inevitable that a number of inaccuracies will appear in a large work such as this, and most of these are of lesser moment. Random examples are: p. 77, according to the authors calcareous sponge spicules are secreted around an axial fiber, but it is doubtful that this is true. In any case, spicules of calcareous sponges do not show an axial canal, and this is not because the canal is destroyed through recrystallization; p. 61, the legend of figure 2–16 should read Eocene-Miocene, instead of Eocene-Oligocene; pp. 123–124, *Lobohelia* is said to form coral reefs in deep cold waters. This form does produce mounds, but they are not reefs in the usual sense. Do the authors consider *all* colonial corals potentially to be reef (hermatypic) corals?; p. 131, the term *coral*, at least by implication applies here as well to soft bodied as to stony anthozoans, but the term is not generally used in this way; p. 379, figure 10–21C, the proper term here

should be prosogyre, not opisthogyre, as indicated; pp. 380–381, prosodetic ligament of pelecypods; is there such type of ligament?

Of much greater importance is a consistent omission or restriction of discussions of general phenomena, or *principles*, which might well have largely displaced much of the traditional material on morphology. Among subjects of great practical and philosophical significance in paleontology the following receive at best only perfunctory attention: variation in animals, homeomorphy, convergence, parallelism, synthetic theory of evolution, functional adaptation, significance of "facies" fossils, environmental modifications, and so on. The single paragraph "fossils as evidence of evolution" on p. 23, subscribes to an outmoded theory of evolution (racial senescence) which has long been discredited and generally abandoned.

In general, both Invertebrate Fossils and Principles are substantial contributions for which the authors and publisher may rightly be proud. It is gratifying that a subject for so long poor in general treatises is now covered by these two comprehensive books. It is a matter for regret, however, that they were written as though they must care for the needs of all academic and professional levels. One or the other might more desirably have been written on an elementary plane.

CORRECTION

In the article by L. von Bertalanffy entitled "Ontogenetic and Evolutionary Allometry," Volume VI, Number 4, an error occurred in Table 1, page 389. In this table read as follows:

Liver, 2nd cycle, $b = 247.5$.
Thymus, 2nd cycle, $\alpha = -0.022$.
Thymus, 2nd cycle, $b = 398.4$.